CALIFORNIA POLLINATION ECOLOGY AND VEGETATION TYPES

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California plant communities which are physiognomically similar but geographically disjunct exhibit remarkable similarities in their pollination dynamics. In contrast, dynamics differ markedly in adjacent communities which do not share a common vegetative structure (Moldenke 1971, 1975). Many parameters of community structure or dynamics (e.g., species diversity, patterns of specialist/generalist food web relations, percent selfing, ploidy levels, percent wind pollination) are not dependent upon the presence of particular species, but are characteristics apparently imposed by climate and/or vegetation, regardless of the flora.

Most attributes of pollination dynamics of California are those generally associated with temperate and semi-arid ecosystems: 1) low diversity of forest trees; 2) moderate diversity of shrub species in scrub communities; 3) high diversity of bee pollinators; 4) low abundance and species diversity of hummingbirds and social bees (except in certain special environments); and 5) generally short blooming periods for most angiosperms, although not as short as those reported in the tropics.

The data presented in this paper are largely based on eight years of research by myself and associates (Moldenke, 1971, 1975 and 1976). A transect was established across central California which incorporated 0.5 km^2 areas of northern coastal scrub, dune scrub, oak-madrone forest, oak woodland, hard chaparral, serpentine grassland, ponderosa pine forest, montane chaparral, mountain meadow, subalpine forest, subalpine marsh-meadow, subalpine talus fell-field and alpine tundra (Moldenke 1975). In southern California, several additional sites were established in coastal sage and dunes, burned and mature chaparral, oak-pine forest and Sonoran Desert scrub (Moldenke 1976, and unpublished data). In all, more than 800,000 pollinators on 2,200 plant species were recorded. In order to establish the veracity of the observed behavior and to permit generalization over a larger geographic extent, a catalogue of the distribution, abundance and host-preferences of all specimens in the major California bee collections has been compiled by Moldenke and Neff (1974).

Table 1.	Alpine Mono Co.	Subalpine: Tioga Pass			Mid-elevation: Mather			Sea Level: Stanford Univ.			
	Tundra	Meadow	Forest	Talus Scree	Grassland	Forest	Chaparral	Chaparral	Forest	Woodland	Grassland
Bees											
(species)	36	36	72	91	146	165	141	176	23	136	163
(individuals)	716	1060	1241	4176	38716	33122	26400	7769	640	2858	19602
Beetles											
(species)	2	10	16	27	37	36	63	101	13	33	47
(individuals)	26	74	4131	1634	51039	27063	119116	93591	2636	20166	57161
Butterflies											
(species)	19	19	15	60	24	26	13	25	2	20	35
(Individuals)	200	37	68	664	2767	1837	3710	669	35	229	3801
Muscoid Flies											
(species)	5	45	44	53	19	9	16	26	0	6	24
(individuals)	94	1416	1588	3485	525	86	321	886	0	202	3345
Syrphid Flies											
(species)	4	7	16	21	18	21	23	17	9	18	22
(individuals)	15	17	83	132	682	69	927	278	47	264	925
Bee Flies											
(species)	4	1	5	9	24	26	10	26	3	11	31
(individuals)	48	2	12	48	4842	4493	26438	2393	350	910	6599
Wasps											
(species)	6	0	4	21	30	23	22	36	1	15	26
(individuals)	7	0	11	141	1100	811	874	245	15	292	448
Hummingbird and Sphyngid Moth											
(species)	2	2	4	4	1	3	2	1	1	1	1
(individuals)	22	6	52	196	20	14	87	202	15	159	31
Total Species	77	158	202	337	326	327	316	484	63	260	386
Total Individuals	1182	5101	10263	13681	100827	68640	170375	115396	6368	30732	98452
Total Biomass	511843	268407	820249	1858722	3477601	3095022	6864100	2526500	293847	1694023	2922640

Table 1. (cont)	Point Reyes Scrub & Dunes	Coastal Sage	San Diego County			
			Burned Chaparral	Chaparral	Montane Forest	Desert
Bees						
(species)	50	80	151	171	135	87
(individuals)	29859	3158	6297	55789	11032	9905
Beetles						
(species)	7	7	16	41	17	24
(individuals)	266	133	4024	4923	3195	570
Butterflies						
(species)	3	3	13	15	13	4
(individuals)	29	68	2732	2750	78	14
Muscoid Flies						
(species)	9	10	11	19	8	5
(individuals)	223	55	417	140	196	755
Syrphid Flies						
(species)	17	4	1	6	3	3
(individuals)	297	15	80	79	180	240
Bee Flies						
(species)	4	7	22	24	16	22
(individuals)	695	261	4200	4989	1470	640
Wasps						
(species)	3	7	38	31	13	36
(individuals)	65	69	335	804	63	453
Hummingbird and Sphyngid Moth						
(species)	1	1	2	2	2	1
(individuals)	45	73	133	187	73	44
Total Species	103	119	254	309	207	182
Total Individuals	31968	3782	18218	69623	16287	12621
Total Biomass	2531785	664993	2236405	3012421	1350936	1530381

TABLE 1. Abundance of Pollinator Groups in California Vegetation Types. Major pollinators within vegetation types as determined at sites 0.5 km^2 in extent. Figures refer to number of insect species and individuals. Biomass estimate based on measurement of length, width and height of each species multiplied by total individuals of that particular species in the census. Flower visiting groups rare in all communities are excluded from the table. From Moldenke (1971 and 1975).

These results must remain somewhat tentative, since conclusions drawn about the flower-visiting preferences of each of the 1,000+ species of bees inhabiting California needs to be corroborated with, at the very least, an analysis of the pollen loads carried by specimens in museum collections. Collection records associated with museum specimens are of course indicative of instances of floral visitation, but bees which exhibit the genetically determined feeding preferences do so for pollen and not for nectar. Hence, since fidelity to source is an important aspect of pollination efficiency, species-specificity of pollen gathering by bees is an extremely significant facet in the dependable pollination of plant genera over large geographic ranges, nearly independent of localized patterns of distribution and competition for pollinators. The conclusions we have reached (Moldenke and Neff 1974) err on the side of the conservative, in general. Particular emphasis has been placed on patterns typical of genera or species groups, when incomplete evidence suggests a deviation from the typical pattern, no conclusions about host-specificity are reached. Hence, instances of specialization by localized populations on abnormal host plants or the specialization by a very rare species on a plant unrelated to the host of a well-known common species, are not recognizable on the basis of our present data base. The general trends cited below, though, are very clear and represent the major features of California pollination dynamics even though we are far from working out all the details of such a comprehensive subject.

In terms of total numbers of species, pollinator diversity in California is highest in hard and montane chaparral, where it is generally 25%-33% higher than in grasslands (Table 1). Diversity is cut by 50% in northern coastal scrub, coastal sage and dune scrub (ca. 105 spp. 0.5 km^{-2}) from that observed in the adjacent chaparral. Pollinator diversity plummets in alpine tundra and mixed-evergreen forest to a low of about 70 spp. 0.5 km^{-2}. On a regional basis, pollinator abundance is highest at Mather (230,000 km^{-2}), drops slightly at Stanford (160,000 km^{-2}, discounting evergreen forest), then falls precipitously to 46,000 km^{-2} throughout San Diego County sites (Table 1). Even lower pollinator densities are noticeable at Point Reyes (21,000 km^{-2}), at subalpine Tioga Pass (18,000 km^{-2}), in mixed evergreen forest (12,000 km^{-2}), and in the alpine tundra at Dore Crest (3,500 km^{-2}). We shall return to this table in the next section.

With few exceptions, the majority of the outcrossed plant taxa in California are visited by many different types of pollinating agents: 71% are visited by at least two distinct pollinator types, 49% by three or more (Table 2). Only the most highly specialized taxa are visited by one type of vector agent exclusively; but even then, the different species within these genera are often serviced by the same vector species. It should be noted that these generalizations about the pollination spectra of California undoubtedly underestimate the degree of broad spectrum syndromes; with the paucity of solid field data and scarcity of published reports, many plant genera cited as primarily pollinated by only one vector type are artifacts of our own studies which were localized in their very nature.

The most important pollinators throughout California are probably hummingbirds, certain bees (e.g., bumblebees, Anthophora and oftentimes semisocial halictine bees), large beeflies (Bombyliidae) and butterflies. These groups vector pollen for considerable distances and/or visit many plant taxa which are ignored by the majority of other pollinator groups. Although specialist bees which visit only a single plant species are seldom of primary importance in the pollination of California plants, under certain circumstances their presence is to the plants' advantage, for these bees will search out their flowers and pollinate them preferentially, even if the plants are in low abundance. The honeybee (Apis mellifera) was introduced into California in the late 18th century and is so widely domesticated and so successful in feral circumstances that it is an integral part of the present pollination ecology of all regions except the alpine tundra and the densest forests. The major effects of Apis have been the competitive local extinction (undocumented but presumably extensive) of many pollinator taxa (especially solitary bees) and the heavy outcrossing of many native plant taxa presumably highly inbred prior to the establishment of dense honeybee populations.

The most frequent and diverse group of insect flower visitors in California are the 1,200 native bee species. Approximately 800 of them are implicated as feeding specialists, programmed to visit only a closely related group of plant species (Moldenke and Neff 1974). Indeed, these specialist solitary bees are often local species-specific pollination specialists, generally active for very short periods (2-4 weeks average), and usually discontinuously distributed but locally abundant. Similar high bee diversity characterized Mediterranean and desert ecosystems throughout the world (Linsley 1958; Moldenke 1976). Since nearly all the plant species serviced by specialist pollinators are visited as frequently (if not more so) by generalist species (84%; Table 2), and since generalist species are often capable of moving considerably longer distances between members of the same species than are the often small and highly localized specialists, competition for vectors usually involves competition for large-bodied, fast-flying, heterothermic generalists. The most successful competitors for these effective vectors often derive a secondary benefit as well; these "polylectic" generalist bee species may utilize a very diverse assemblage of plant species across the broad expanse of their distribution, at a given site they often facultatively specialize upon whatever local resource provides the best reward, facilitating the effectiveness of the pollination syndrome markedly.

At least ninety-one genera of California plants have coevolved with specialist solitary bees that are restricted to species of that particular genus or a very closely related plant genus. Additionally, 68 plant genera are known to be strongly associated with solitary bees that are family-specific, particularly to the Compositae and the Papilionoideae, in their host preferences. With very few exceptions, the larger the number of specialist vectors that a plant genus is serviced by the larger is the number of generalist pollen vectors as

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TABLE 2. Pollination Syndromes of the California Flora. Vector categories represent the most efficient modes of pollination for a particular plant genus rather than simply the total flower visitors. Every effort was made to limit the total categories applicable for each genus to exclude an emphasis on infrequent flower visitors. Conclusions are based on my own research at defined sites throughout the state, consultation with colleagues and the results of our bee catalogue (see Appendix).

A. Only categories with listings more than 5 included in table;
B. Indicates pollination by indicated mode and at least two others;
C. Indicates pollination by indicated mode and at least one other;
D. Obligate selfing is a subset of habitual selfing;
E. Difficult to delineate between modes without further investigation (57 taxa cited jointly).

Table 2.

POLLINATION MODE																
Water Pollination	Wind Pollination	Obligate Selfer Ⓓ	Habitual Selfer Ⓔ	Generalist Bees Ⓔ	Specialist Bees	Hummingbird	Sphinx Moth	Moths (nocturnal)	Butterflies	Wasps	Beetles	Muscoid Flies	Beeflies	Syrphids	Primitive Flies	# California Genera Possessing Stated Mode of Pollination Ⓐ
X																5
	X															136
		X														76
			X	(x)												246
			(x)	X												66
				X	X											27
					X											9
						X										10
				X		X										22
							X									3
								X								4
									X							2
										X						0
				X						X						5
											X					1
				X							X					9
												X				5
				X								X				4
													X			5
				X									X			15
				X	X								X			7
														X		0
				X										X	X	18
															X	6
				X		(← 2 x →)										49 Ⓑ
				X	X	(← 1 x →)										20 Ⓒ
				X	X	(← 2 x →)										70 Ⓔ
	X			(← 2 x →)												5 Ⓑ
						(← 2-5 x →)										27

well. Exceptional genera pollinated almost exclusively by specialist bees are Calystegia, Camissonia, Coldenia, Collinsia, Cucurbita, Euphorbia, Physalis and Zigadenus.

The dominant form of pollination in all but the desert and chaparral communities is, of course, anemophily, as it is throughout the temperate and subarctic zones of the world. There are very few groups of wind-pollinated plants endemic to California; most of our taxa are very widespread and their pollination adaptations do not seem to be peculiar to California.

Eighteen percent of the angiosperm genera with non-anemophilous flowers are unsuccessful at, or at least inconsistent in, attracting abundant pollinators. These genera seem to be consistently selfed, though under certain unusual situations they may be efficiently outcrossed. Many of these genera are endemic to California and presumably evolved under conditions of pollinator abundance similar to those observed presently (e.g., Achyrachaena, Allophyllum, Amblyopappus[a], Apiastrum, Athysanus, Downingia, Eatonella, Emmenanthe, Gayophytum[a], Nemacladus, Pectocarya[a], Plagiobothrys[a], Psilocarphus[a]). Endemic origin of some obligately selfing taxa is pronounced in more widely spread plant genera usually characterized by genetic self-incompatibility and heavy visitation rates (e.g., Astragalus, Eriogonum, Lasthenia, Layia, Lotus, Lupinus, Mimulus, Orthocarpus).

POLLINATION CHARACTERISTICS OF VEGETATION TYPES

Forests

The low diversity of the varied forest types of California permits successful wind pollination. As Bateman (1946) and Colwell (1951) have shown, wind pollination is normally extremely inefficient. The success of wind pollination decreases with the cube of the distance between plants, and for trees more than 100 feet apart, the chance of successful pollen transfer becomes vanishingly small, even considering the astronomically large number of pollen grains produced. Successful wind pollination can be increased by decreasing the surface area of nonstigmatic surfaces, through such evolutionary adaptations as needlelike or filiform leaves (conifers, Artemisia californica) and leaflessness (some Quercus, Platanus, Fraxinus) at the time of pollination. Three of the four nonwind-pollinated forest tree

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[a] California evolutionary origin with subsequent "sweepstakes colonization" of Chile (Raven 1963).

species in California (Arbutus, Umbellularia, Acer) occur in the diverse mixed evergreen forest, in which wind pollination would be a severe disadvantage.

Within the understory, cross-pollination is a function of sun-dappling (Beattie 1971). Nearly all forest floor pollinators are most active in direct sunlight; neighboring shaded plants as little as 15 cm away are seldom if ever visited. Forest floor pollinators for whom this behavior is characteristic, particularly bees and butterflies, still must be able to fly between the sun-dapples in order to exploit sufficient resources for sustained activity. The most abundant and significant pollinators of the forest floor are bumblebees and Bombylius major, a beefly. Their activity is maximized by a facultative homeothermy (Heinrich 1974), which allows sustained flight within shade in order to locate a maximum number of thermally advantageous sunny spots. These insects are characterized by very low surface/volume ratios; dense, dark, absorptive insulatory pubescence; and large body size necessary for the maximal conservation of metabolically produced heat. The bees, Andrena and Nomada, and the nematoceran and muscoid flies --also responsible for much California forest pollination --are poikilothermic.

Compatibility studies have rarely been undertaken on wind-pollinated tree species. Most species are monoecious (conifers, Quercus, Platanus), an adaptation clearly designed to promote outcrossing. It is not known whether selfing is possible or whether, if possible, selfed seed competes favorably with outcrossed seed of the same species. Genetic fine-tuning to the environment is a well-documented result of outcrossing (hybridization) in the oaks of the Santa Lucia Mountains (Griffin 1973).

Forest understory species are mainly perennial geophytes or sprawling woody subshrubs or vines; annuals are rare except in the most open savanna forest types. In all low-elevation forests, nearly the entire understory blooms exclusively in early spring. Most of these plants are derivatives of the widespread Arcto-Tertiary Geoflora and have evolved anthesis periods synchronous with the maximum probability of light-dappling, prior to leafing-out and the replacement of winter-killed branches. Most of these forest floor perennials are genetically self-incompatible and obligately require outcrossing vectors. There are no confirmed specialist vectors[b] in these environments, and the pattern of synchronized blooming places plants in strong competition for vectors. In order to maximize the visibility of flowers on the forest floor, natural selection has acted convergently to produce a flora with an overwhelming preponderance of white flowers, a rather uncommon flower color in most other native plant communities. Recognition by distinctive scents accounts for the specialized pollination syndromes of the brownish-flowered Asarum, Aristolochia and Scoliopus.

In the north coastal forest, pollinators of any sort are extremely infrequent. All the major groups appear to be entirely absent. In the narrow riparian coastal forests, pollinators may stray in from surrounding communities (hummingbirds for Lilium, Aquilegia; bumblebees for Oxalis, Arbutus; Bombylius major for Trientalis, Collomia), but in the midst of large expanses of conifer forest they are virtually absent. The major pollinators in these situations probably are primitive nematoceran gnats and midges and occasional bumblebees. Bumblebees inhabiting these regions are so infrequent that they have not been well-studied; there may be special forest-adapted species (perhaps Bombus caliginosus, B. sitkensis) that are able to locate flowers in low-light conditions and characteristically have very small colony populations due to the brevity of the blooming season. The only frequent flower visitors in these situations are the primitive flies. Their extremely small size and poor powers of flight apparently render them extremely inefficient pollen vectors, but under conditions in which they are the only potential vectors, they presumably exert a major vector influence in the community. Asarum (Vogel 1973) and Aristolochia are pollinated by fungus gnats attracted to the flower by scents resembling their normal mushroom food sources.

In the mixed evergreen forest of the Coast Ranges, there are many more herbs on the forest floor and considerably more sundapples. Pollinators are infrequent, but bumblebees (Bombus spp.), beeflies (Bombylius major), and solitary bees (Andrena spp. and its inquiline cuckoo-bee parasite, Nomada spp.) are the most significant

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[b] Several species of as yet unstudied solitary bees may be found to be at least facultative specialists in localized regions (e.g., Andrena nigrihirta on Dentaria californica and Dialictus ornduffi on Jepsonia.

vectors. All vectors are active primarily in the earlier spring; none are known to be specialists. The most massive floral resource is *Arbutus menziesii*. Within the forest it is pollinated primarily by *Bombus edwardsii*, although long-distance pollination by nectar-feeding chickadees and hummingbirds is significant. Unlike most other bumblebee species, *B. edwardsii* along the central coast may remain active all winter long, presumably existing on stored food harvested during the previous season, and is apparently at maximum colony size during the *Arbutus* bloom, at which time it produces enormous quantities of sexuals and disbands to start new colonies (Moldenke, unpublished data).

In the montane and subalpine forest belts, forest floor pollination is primarily mediated by bumblebees and the solitary *Osmia* bees. *Osmia* is primarily associated with legumes (*Vicia*, *Lathyrus*, *Lupinus*) and composites (*Wyethia*, *Helianthella*, *Agoseris*) and is most abundant in areas of disturbance or regions bordering mountain meadows. *Osmia* carries the collected pollen on the undersurface of its abdomen and hence is an extremely efficient pollinator of the upward projecting stigmas of these two plant families. Numerous species of bumblebees reside in montane forests and visit nearly all flower types; they are most abundantly associated with the Leguminosae, Rosaceae and Compositae. With increasing altitude, bumblebees become much less abundant as much of the forest understory drops out; nevertheless, they assume nearly the entire pollination function as most other vector types drop out completely. *Andrena*, *Nomada* and *Bombylius* are important, especially at altitudes less than 2,000 meters.

In more open montane forest types (e.g., ponderosa pine), a great deal of direct sunlight reaches the forest floor and a much wider diversity of flower types and colors exists than in the previously discussed forest types; annual plants are often abundant. Pollinators generally are not specialists; if so, they are usually specialists to the family level only (roses, legumes, composites). In the most open forest types, such as oak-woodland, understory plants aften assume at least ninety percent cover and pollinators of all groups are abundant. Wind pollination is frequent in the understory, with few self-incompatible outcrossing species (e.g., *Bromus laevipes*), but numerous self-compatible facultative selfers (e.g., *Festuca*, *Stipa*, *Elymus*, most annual *Bromus*). Butterfly (composites, *Monardella*) and hummingbird (*Grossularia*, *Ribes*, *Delphinium*, *Monardella*, *Penstemon*, *Erysimum*) pollination

Table 3.	CENTRAL CALIFORNIA										
	Dore	Tioga Pass			Mather			Stanford University			
	Alpine	Subalpine			Mid-elevation			Sea Level			
	Tundra	Meadow	Forest	Talus Scree	Grassland	Chaparral	Forest	Chaparral	Forest	Oak wdld	Grassland
Solitary Bee	20 27%	13 9%	26 19%	38 20%	40 40%	37 62%	56 30%	41 42%	18 17%	60 45%	59 41%
(Specialist Bee)	11 15%	9 6%	14 10%	27 15%	28 28%	22 37%	23 13%	18 19%	2 2%	21 16%	29 20%
Halictine Bee	/	4 2%	13 9%	30 17%	7 7%	8 13%	10 6%	13 14%	5 5%	11 9%	20 14%
Bumblebee	18 24%	22 15%	26 19%	40 22%	12 12%	28 47%	37 21%	8 8%	19 18%	19 15%	16 10%
Beefly	/	/	2 2%	9 5%	16 16%	14 23%	32 17%	12 12%	9 9%	18 15%	29 20%
Beetle	/	/	6 5%	10 6%	13 13%	9 15%	9 5%	19 20%	5 5%	14 10%	24 16%
Wasp	1 1%	/	/	1 0%	2 2%	5 7%	5 3%	5 5%	2 2%	4 3%	2 1%
Butterfly	6 8%	2 2%	4 4%	15 8%	13 13%	12 20%	7 4%	7 7%	1 1%	3 3%	13 7%
Moth	2 2%	1 1%	/	2 1%	2 2%	/	/	2 2%	/	3 3%	1 1%
Muscoid Fly	4 5%	24 16%	20 16%	15 8%	3 3%	1 1%	3 2%	6 6%	/	2 2%	4 3%
Syrphid Fly	1 1%	3 2%	/	4 2%	4 4%	2 3%	2 1%	7 7%	6 6%	11 9%	7 4%
Hummingbird and Sphyngid	3 4%	3 2%	6 5%	11 6%	1 1%	7 12%	5 3%	7 7%	3 3%	7 6%	4 3%
Wind	19 25%	50 35%	37 29%	38 20%	31 31%	7 12%	22 12%	11 12%	20 19%	25 18%	23 16%
Habitual Selfer	29 39%	28 19%	30 22%	65 35%	42 42%	4 7%	47 25%	14 15%	19 18%	29 22%	57 41%
(Obligate Selfer)	2 3%	7 5%	2 2%	15 8%	4 4%	1 1%	6 4%	4 4%	5 5%	7 6%	27 18%
Apomictic	6 8%	11 8%	7 6%	12 7%	/	/	2 1%	1 1%	1 1%	/	1 1%

Table 3.(cont.)	CENTRAL CALIFORNIA		SOUTHERN CALIFORNIA				
	Pt.Reyes	Farallon Is	Torrey P.	Descanso		Laguna	Ocotillo
	Sea Level						
	Scrub Dunes		Coast Scrub	Chap. Burn	Chap-arral	Mont. For.	Des-ert
Solitary Bee	23 12%	/	37 27%	35 24%	32 41%	33 41%	34 29%
(Specialist Bee)	9 5%	/	24 18%	18 12%	20 29%	16 20%	24 21%
Halictine Bee	18 9%	/	10 7%	8 5%	5 7%	1 1%	2 2%
Bumblebee	81 40%	/	/	/	/	/	/
Beefly	5 3%	/	3 2%	11 7%	4 6%	7 9%	2 2%
Beetle	4 2%	/	4 3%	3 2%	/	3 4%	3 3%
Wasp	1 1%	/	1 1%	8 5%	2 3%	2 3%	5 4%
Butterfly	2 1%	1 3%	3 2%	4 3%	1 1%	1 1%	2 2%
Moth	/	/	/	/	/	/	/
Muscoid Fly	3 2%	3 9%	1 1%	1 1%	2 3%	1 1%	3 3%
Syrphid Fly	6 3%	6 18%	3 2%	3 2%	/	/	4 4%
Hummingbird and Sphyngid	7 4%	/	4 3%	8 5%	10 14%	6 8%	3 3%
Wind	32 16%	3 9%	21 15%	16 11%	7 10%	16 20%	13 11%
Habitual Selfer	60 30%	31 93%	45 33%	35 24%	6 9%	10 13%	44 38%
(Obligate Selfer)	22 11%	9 27%	12 9%	9 6%	1 1%	3 4%	7 6%
Apomictic	4 2%	/	/	/	/	/	/

TABLE 3. Pollination Syndromes of California Vegetation Types. Major pollinators within vegetation types as determined at sites 0.5 km^2 in extent. Figures refer to number of plant species and percent of the resident flora. Pollinators utilized are those actually observed, rather than speculation based on flower morphology. Percentages sum to more than 100% since some species utilized more than one mode as their usual pattern of reproduction. Specialist bees represent a subset of solitary bee statistics; obligate selfers represent a subset of habitual selfing. From Moldenke (1971, 1975).

assumes an important role. Species diversity of both angiosperms and pollinators (particularly bees) approaches the high levels found in the Mediterranean scrub and grassland (Table 1).

Chaparral: hard and soft

Wind pollination rarely occurs among the shrubs and subshrubs of chaparral (Artemisia, Garrya are exceptions); only along the fog-shrouded coast, where pollinators are very scarce, does wind pollination occur for a dominant species (Table 3). Though wind pollination would be facilitated by the low diversity of dominant shrubs, insect and bird pollination is the rule, just as it is in the physiognomically analogous matorral of Chile (Moldenke and Neff, in press). Abundance of insects associated with flowers and species diversity of pollinators are extremely high even in small regions (484 species of flower visitors in chaparral at the Stanford University site), eight times the number of species in the adjacent forest and eighteen times the number of individual insect vectors observed. Such extremely high diversity and abundance of pollinators must result in a very strong over-all competition by pollinators for plant species. Nearly all chaparral dominants are associated with specialist pollinator taxa. Nevertheless, competition among plant species for some of the more mobile and extremely common generalist pollinators has resulted in the evolution of distinct, mutually exclusive anthesis times (Mooney, 1972; Moldenke, unpublished data). This exclusivity of blooming periods is facilitated by the extremely large root systems of Mediterranean scrub species (Mooney,1972), enabling scrub species to tap stored water supplies well into the summer drought. Species that have been forced to bloom in the earliest part of the year, when it is frequently too wet and cold for pollinator activity, are extremely poorly pollinated and are self-incompatible (e.g., Osmaronia, Dirca); they are not associated with specialist pollinators.

Almost all chapparal shrubs are genetically incompatible, or, if compatible (e.g., Diplacus) or undetermined (e.g., Eriodictyon), they are heavily outcrossed by extremely abundant pollinators and possess mechanical adaptations which decrease the potential for selfing. Most chaparral shrub species are very heavily visited by pollinators; all groups are present in abundance. Aesculus is of particular interest because it is pollinated by butterflies (Euphydryas, Strymon) and sphyngid moths. All species of Aesculus secrete a nectar that is poisonous to bees, interfering with the normal development of the larva (Benseler, 1968).

The most significant features of the chaparral permitting the extraordinary abundance of bee species are the absence of ground cover, providing ample nesting sites for ground-nesting species, and the frequency of fires, which continually renews supplies of dead branches for twig-nesting species. In mature chaparral, the very few annuals which occur under the canopy are self-compatible and extremely heavily outcrossed by nectaring bees or parasites patrolling suspected bee nest sites. Just after a burn, annuals and geophytes represent the entire floral resource. Most species are capable of selfing and usually are forced to do so in the absence of large numbers of recolonizing pollinators, though some of the most abundant species are genetically incompatible (e.g., Brodiaea, Corethrogyne, and certain species of Orthocarpus, Salvia, and Amsinckia). However, within two to three years after a fire, large pollinator diversities build up (Moldenke and Neff, 1976) and some species of fire-sprouted forbs are then heavily visited by specialist and generalist vectors in great abundance (e.g., Phacelia, Lotus, Lupinus, Penstemon). Emmenanthe penduliflora, an obligate fire-sprouted annual, is usually limited in appearance to the very first year after a fire; two specialist bee pollinators (Protodufourea wasbaueri and Conanthalictus seminiger) have coevolved with this plant. Since the bees are not known to remain in aestivation until activation by fire, it is unclear how they are capable of relocating a resource during subsequent years or how this association might have originally evolved.

Unlike most other California vegetation types, the chaparral exhibits some nocturnal moth pollination (Aesculus, Adenostoma, Heteromeles, Prunus)associated with masses of small white flowers. There are often large populations of bumblebees, which are particularly significant as pollinators in the cool, early spring. At Mather, I have even observed queen bumblebees foraging on Arctostaphylos during a clear night at midnight with 15 cm of snow still on the ground. There is often a high diversity and abundance of halictine bees (oftentimes semisocial colonial units) in chaparral, which are efficient pollinators when facultatively specialized due to the nonoverlapping anthesis seasons. Sphecid wasps are frequent flower visitors in the Sierra Nevada.

Grasslands

The floral productivity of California grasslands varies greatly from year to year as a function of rainfall. Harvester ant seed predation also continuously alters the distribution and relative abundance of flower types. Under all conditions, anemophily is the dominant form of pollination. Though only 16%-31% of the species are wind-pollinated in any local region, most of the dominant species, comprising 20%-40% of the floral biomass, are wind-pollinated. The grasslands were originally dominated by Stipa, which is apparently heavily outcrossed, although genetically capable of selfing. Nearly all the common grasses today, including the introduced weedy species, are generally outcrossing facultative selfers, exceptions being Koeleria cristata, Poa scabrella, and Lolium perenne, which are genetically incompatible. The diminutive species often found in serpentine areas (Festuca spp., Plantago erecta) are often cleistogamous, as are many of the small individuals of Bromus mollis. Certain dominant grassland forbs are genetically incompatible (e.g., Lasthenia chrysostoma, Layia platyglossa, Eschscholzia californica, Orthocarpus densiflora, Brodiaea spp.). But the overwhelming majority of species are compatible (79%; Moldenke 1971).

Habitual selfers are most abundant in grassland communities (41%-42% of the serpentine grassland flora at Stanford and the mountain meadow at Camp Mather; Table 3). Many of these habitual selfers are in reality obligate cleistogamous selfers (Achyrachaena mollis, Astragalus gambellianus, Lupinus concinnus, Lepidium nitidum, Amsinckia menziesii, Orthocarpus pusillus). Eighteen percent of the species are obligate selfers, a level in excess of that observed in other vegetation types, and approached only by the annual constituent of the dune scrub and coastal sage (9%-17%). Obligate selfers in grasslands usually bloom before the period of activity of the pollinators. At Stanford, pollinator diversity and biomass starts to rise noticeably during the first week in April; by this time, 68% of the 27 obligate selfers have nearly finished blooming.

The usual grassland pollinators are solitary and semisocial bees, beeflies and butterflies. Hummingbirds are scarce (present on Delphinium spp. and Salvia carduacea). Nocturnal pollination is very infrequent. There are generally large numbers of specialist-feeding pollinators. Many sympatric, congeneric specialist bee species occur on the dominant species, particularly Andrena in the spring and Megachile and Melissodes in the summer; the mechanisms by which they escape extinction through competition are unknown. Whether the high diversity of pollinators confers any type of pollination benefit to the plant (such as predictability under all climates) is also unknown. Most of the pollinator groups associated with California grassland communities are derived from basic Nearctic pollinator stock, except for some of the later summer groups, which have evolved from the fauna associated with Tropical Middle American and Madro-Tertiary Geofloras (Moldenke 1976). Diversity of pollinators in native grasslands is extremely high. Many species are extremely abundant but often highly localized. Diversity often increases in oak savanna habitats as the shade extends the length of the blooming seasons and branches permit the existence of twig-nesting solitary bees.

Hot Deserts

Annual variability of floral production is extreme in desert ecosystems. Paradoxically, years characterized by abundant annual plants are usually characterized by extremely few pollinators; years of low precipitation and few flowers are apparently characterized by high diversity and abundance of pollinators. Entomologists have long wondered whether these observations were the artificial result of an alternating concentration and dilution effect produced by the distribution of resources, or if the observations reflected the real abundance of pollinators. My own studies and unpublished ones of Neff imply that the real abundance of pollinators does indeed fluctuate greatly from year to year. Years of cool, wet winters are most propitious for C_3 annual plants; however, cool weather is thermally most difficult for the activity of cold-blooded pollinators.

High winds characteristic of spring on the Colorado and Mojave Deserts are very detrimental to pollinator activity. Nearly all the dominant plants are genetically incompatible and outcrossed during years of high pollinator abundance. Nearly all the annual plants (exceptions include Camissonia, Oenothera) are genetically compatible and the great majority of populations self in all but the years of pollinator abundance. Floral size diminishes and genetic compatibility evolves as widespread angiosperm genera enter desert regions (e.g., Eschscholzia californica/E. minutiflora).

Desert regions are characterized by high bee diversity over a wide geographic extent, but on a small scale fewer species are present (87 in 0.5 km^2) than in the chaparral (161 species), grasslands (153 species), or open montane forest (145 species; Table 1). More than 60% of the desert bee species are probably specialist feeders; they are associated with both perennial and annual floristic elements. In addition to solitary bees, beeflies and wasps play an important role in desert pollination systems. Hummingbirds are rare in deserts and are usually confined to mountain canyons where trees and shrubs may tap significant water flow. There, the syndrome of the large, nectar-laden flower coevolved with hummingbirds, is evident in such taxa as Fouquieria, Agave and Chilopsis.

In regions of bimodal rainfall, the summer and winter annuals are confined to only one season by germination and metabolic requirements. Similarly, most pollinators are limited to one or the other blooming season; spring season bees are generally derived from the Nearctic fauna while summer season bees are often Neotropical in derivation (Linsley 1958). There are no common large supergeneralized pollinators active in both seasons in the deserts of California. Even bees that are active in both rainy seasons (some Colletes and Perdita obliqua, a Prosopis specialist) produce two distinct generations during the year (Simpson et al. 1976).

Wind pollination is confined to several shrubs (e.g., Simmondsia, Franseria), infrequent subshrubby perennials (e.g., Stillingia, Tetracoccus), and grasses that bloom in response to summer rains. The shrubs have evolved either monoecy or dioecy to facilitate outcrossing; the grasses are often cleistogamous. Many of the Amaranthaceae and Chenopodiaceae in the shadscale scrub and alkalai sink communities are wind-pollinated but apparently habitually self when present in low density.

Two special features of desert pollination in California are crepuscular pollination and the substitution of oils for flower nectar. Several desert plants open their flowers in the late afternoon or the very early morning (e.g., Onagraceae, Cucurbitaceae, Nicotiana, Hesperocallis). Before the flowers wilt during the heat of the desert day, they are pollinated by large, heavily insulated, facultatively thermoregulatory insects such as sphinx moths and bees of the genera Peponapis, Xenoglossa, Xylocopa, Caupolicana and Andrena (Onagandrena). Crepuscular pollination in the other regions of California is limited to closely related species descended from these desert plant taxa, exceptions being Aesculus and Chlorogalum. The Krameriaceae and Malpighiaceae are pollinated exclusively by female Centris (Paracentris) bees, which collect the oil produced by these plants as provision for their young (Simpson, Neff and Siegler 1977).

Alpine and subalpine vegetation types

Alpine regions of California are characterized by several distinct types of pollination systems (Moldenke 1975). In all of them, the relative percentage of generalist pollinators, by individual count or biomass, is extremely high, while total diversity of all pollinator groups is very low, especially beeflies and solitary bees. Anthomyiid flies, butterflies and bumblebees are the groups effecting most pollination.

The strongest emphasis on anemophily in California occurs in subalpine marsh-meadows, where 41% of the species are wind-pollinated. High diversity of sedges, rushes, and grasses militates against efficient wind pollination; however, most species are genetically compatible (all Juncus, Luzula, monoecious Carex and most alpine grasses) and capable of apomictic propagule or vegetative propagation. Except for the locally abundant Heleocharis pauciflora, which occurs on shifting gravel banks of mountain meanders, all marsh-meadow residents are rather long-lived perennials. Reproduction by seeds is apparently extremely infrequent.

Pollinators are virtually absent in marsh-meadows. Nearly all insect pollination occurs through the agency of extremely inefficient (very poor flower constancy) anthomyiid flies of the genera Hylemya, Pogonomyia and Lasiops. Occasional bumblebees and butterflies stray into the marshes and, as individuals, probably accomplish a level of outcrossing equivalent to several hundred flies. Widespread composite genera abundantly visited by diverse insect pollinators are represented in the marshes by predominantly selfed species (Senecio subnudus, S. pauciflorus and Erigeron lonchophyllus). Normally outcrossed taxa (i.e., Castilleja culbertsonii, Pedicularis groenlandica) are much more frequently visited by bumblebees when growing only a few feet away from talus communities than when they occur centrally in marshes.

Talus scrub communities are characterized by a low diversity and abundance of pollinators, when compared to lower elevations; nevertheless, they support most of the species (86%) and nearly a majority of the pollinator individuals (49%) found in high alpine situations (Moldenke 1971, 1975). By species count, the largest number of bees are specialist flower pollinators, but all of them are so rare as to comprise collectively only 28% of the bee fauna by biomass. Their extremely low population sizes and patchy distributions indicate that they apparently suffer frequent local population extinction and must recolonize. Most specialist taxa in the high alpine community types of the Sierra Nevada are apparently derived from the Great Basin (e.g., Anthocopa spp., specialists on Penstemon) and are characterized by wide elevational distributions on the east face of the Sierra Nevada. There are no moderately specialized bee species (oligophags); such species are abundant at low elevations, where they account for about 60% of the bee fauna. At middle elevations, generalists, extreme specialists and oligophags are equally represented (Moldenke 1975). At extreme elevations, however, climatic fluctuations are so severe and unpredictable that the jack-of-all-trades generalist is the most efficient competitor in light of fluctuating plant abundances.

Though floral biomass is not pronouncedly reduced over levels censused at lower elevations, pollinator abundance is much lower in subalpine vegetation types (115,000 individuals in chaparral scrub at Stanford; 13,000 individuals in talus scrub at Tioga Pass; Moldenke 1971, 1975). Very severe competition among flowering plants for the available pollinators results in many species remaining unvisited. Self-compatibility among perennial plants reaches its highest levels ($\overline{X}$ = 80%) in high-elevation California. Many plants are forced to self habitually (45%) and apomictic reproduction is frequent (Moldenke 1975). Some species in normally entomophilous genera and many apparently anemophilous plants are entirely cleistogamous or apomictic (e.g., Poa rupicola, Melica bulbosa, Erigeron compositus, Calamagrostis purpurascens, Arnica spp., Antennaria spp.). The very strong omnipresent winds militate against wind pollination and produce physiologically stressful conditions for flying insects. Pollinator taxa at altitudes of more than 4,000 m are usually species distributed in the far north of Canada as well.

The uniqueness of the breeding systems of the alpine flora is apparent in an examination of ploidy levels. Nearly 78% of the flora (Moldenke 1973, 1975) is polyploid. Furthermore, many of the taxa are greater than hexaploid. Though there are many explanations proposed for the evolution of polyploidy, the correlations Stebbins (1971) draws between polyploidy and the cyclic glaciation of the Sierra Nevada seems the most ecologically relevant.

Floral diversity measured in terms of *H*[c] is noticeably higher in alpine communities than at lower elevations (average of all communities at Stanford, 2.62; Mather, 2.82; Tioga Pass, 3.19; and Dore Crest, 3.26). Since disproportionate relative abundances decrease values of *H* diversity, and since such disproportionate census counts are usually correlated with annual plants, this increasing floral diversity value at higher altitudes can be shown to be directly correlated to decreasing abundance of annual plants at higher altitudes. Annual plant species comprise 21% of the flora at sea level, 15% at 1,300 m, 6% at 3,000 m and were not observed at altitudes of 4,000 m.

Coastal vegetation types

Portions of the northern coastal scrub, coastal sage, coastal prairie, salt marsh and dune communities on the windward slope of the Coast Ranges or along bluffs adjacent to the ocean, have an exceedingly depauperate pollinator fauna and for convenience are best considered together here.

Coastal pollination conditions are similar to those in the high alpine except that the blooming season is not shortened. Moderating ocean breezes and generally omnipresent wind and fog hamper poikilotherm pollinator activity. On coastal bluffs and stabilized dunes, pollination is generally limited to thermoregulatory bumblebees, *Anthophora* bees, and hummingbirds. From Point Lobos northward, the majority of the pollinators are disjunctly distributed in the High Sierra Nevada as well and thence continuously northward to Alaska and the Northwest Territories (Stephen 1955). Inland of immediate coastal exposure, the pollinator fauna of northern coastal scrub and coastal sage shifts to a depauperate chaparral fauna of very low density.

Wind pollination predominates in all salt and estuarine marshes; chasmogamous marsh forbs are pollinated by muscoid flies and bembicine sand wasps (E. Schlinger, pers. comm.) but nearly all are capable of habitual selfing. The muscoid flies and the occasional small-bodied solitary bees which live along the coast are restricted in the time of day and the number of days in which they can be active, by the presence of coastal fog. As one moves northward along the Pacific Coast, pollinator activity decreases and along with it total species abundance (79 solitary bee species at Torrey Pines,

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[c] $$H = -\sum_{i=1}^{s} (\text{relative abundance}_i)\,(\ln \text{relative abundance}_i)$$

42 species at Point Reyes).

Unlike alpine environments, in which the total growing season for perennials is severely limited, many species of self-incompatible coastal perennials (e.g., *Lupinus arboreus*, *Mesembryanthemum chilensis*, *Eriophyllum staechadifolium*, *Eschscholzia californica*) are able to set outcrossed seed in this pollinator-poor environment by extending the period of anthesis nearly year-round. Annual plants, abundant under the canopy of the coastal scrub, respond to the perpetual lack of pollinators by the evolution of cleistogamy and obligate selfing; 10% of the coastal flora is cleistogamous while only 5% is cleistogamous in the chaparral. Showier flowers are required even for limited outcrossing in coastal exposures, where pollinators are limiting (e.g., *Epilobium watsoni*, *Oenothera hookeri*, *Amsinckia spectabilis*, *Plagiobothrys reticulatus*, *Orobanche grayana* var. *violacea*, *Mimulus guttatus* var. *grandis*) than are required by closely related taxa in the chaparral where heavy outcrossing can be achieved with minimal floral size.

Offshore pollination has been studied at the Farallon Islands (Moldenke 1971 and 1975). Nesting oceanic birds (e.g., *Larus occidentalis*) utilize every scrap of vegetation and flotsam for nest-building; therefore, the flora is restricted to annual plants which must bloom and produce mature seed prior to the gull nesting season beginning in late April. During this period, drizzle and strong winds are frequent. The usual pollinator groups are entirely absent except for one species of migratory butterfly (*Vanessa cardui*) and an abundant hoverfly. All the native species and successful introductions are genetically compatible and selfing is the usual method of reproduction for all of them. The beaches and surrounding rocky ridges are inundated with "clouds" of seaweed flies (*Fucellia evermanni*); some of these flies visit the flowers of *Spergularia macrotheca* and *Lasthenia minor* ssp. *maritima* and may vector pollen between individuals. Along the immediate mainland coast *L. minor* is self-compatible, but it is outcrossed by locally frequent but unpredictable vector species (the largest, blackest, and hairiest of the specialist pollinators, *Andrena chlorosoma*, in particular). *Lasthenia* species of the interior grasslands are genetically incompatible and heavily visited by specialists as well as generalists. However, on the offshore islands, pollinators are virtually absent and *L. minor* has nearly lost its attractive ray florets and is generally self-pollinated before the disc florets have opened. Lasthenia glaberrima of the marshes has also lost its ray florets and incompatibility in the absence of its normally abundant bee pollinators (Ornduff 1966).

COMPARATIVE FEATURES OF POLLINATOR AVAILABILITY

No instances within the California flora are documented in which the distribution of a plant species is limited by absence of a suitable pollinator. Nevertheless, over long periods of time the relative abundance and diversity of different pollinator groups must exert a major effect on the success of various plant taxa. Table 3 presents the results of my own studies on the relative abundance of pollinator types in 19 California plant communities.

Bees are the most diverse group of pollinators in all the communities studied except the subalpine marsh-meadow (36 species per 0.5 km^2), where anthomyiid flies are most diverse. Anthomyiid flies are as diverse in the other subalpine communities (ca. 45-55 spp.), but bee diversity is proportionately even more diverse (ca. 70-90 spp.). Bee species count reaches its highest levels in low elevation and mid-elevation grassland chaparral and open forest communities (140-170 spp. per 0.5 km^2). Bees generally outnumber (by individuals) all other pollinator groups at the sites; however, beetles are the most abundant groups in chaparral (Stanford and Mather), oak-woodland (Stanford) and montane grassland (Mather) while anthomyiid flies and sawflies outnumber bees in subalpine meadows and forests. Butterflies are most abundant in grasslands (ca. 25), chaparral (ca. 25) and subalpine talus (ca. 50); they are very infrequent in desert (4 spp.) and the coastal sage (3 spp.) of northern California. Beeflies average about 20-30 spp. per o.5 km^2 throughout California, but are very reduced throughout elevations above 2,000 m, the immediate coast and forest communities. Beefly abundance is highest in chaparral and grassland communities, reflecting the extreme abundance of Conophanus on Lasthenia, Geron on Eriogonum and Phthiria on Ceanothus. Syrphid fly diversity averages 15-17 spp. per 0.5 km^2; generally reduced levels are found throughout the southern transect and specific reductions are observed in subalpine marsh-meadow and mixed evergreen forest. Hoverflies are most abundant in serpentine and mid-elevation grasslands and mid-elevation chaparral. Eupeodes volucris, a generalist, is an extremely important pollinator of the early spring Colorado Desert ecosystem. Wasps are abundant flower visitors in many California communities (except for alpine and coastal regions) and characteristically demonstrate the highest diversity levels in Mediterranean and desert scrub. Hummingbirds and sphinx moths are undiverse throughout all California; they occur in highest abundance in the chaparral and talus scrub communities, where deep tap-rooted shrubs provide them with the most predictable resources.

Hummingbird, sphyngid and bumblebee abundance is subject to extreme fluctuation seasonally and annually. Hummingbirds and the most abundant sphyngids are migratory; they are limited to the spring season in desert regions, building up to their highest abundances in the alpine communities by late summer. Bumblebees are variable in abundance in all regions; factors controlling their abundance have not yet yielded to analysis.

Total pollinator diversity is highest in scrub communities in all locations, generally 25%-33% higher than grasslands. Diversity is cut by 50% in coastal communities (ca. 105 spp. per 0.5 km^2) from that observed in adjacent chaparral. Diversity plummets in arctic-alpine and mixed-evergreen forest to a low of ca. 70 species. Pollinator abundance is highest at Mather ($\bar{X}$ = 230,000 km^{-2}), drops slightly at Stanford (160,000 km^{-2} discounting evergreen forest) and then precipitously to 46,000 km^{-2} at San Diego, 21,000 km^{-2} at Point Reyes, 18,000 km^{-2} at subalpine Tioga Pass, 12,000 km^{-2} in mixed-evergreen forest and 3,500 km^{-2} in the arctic-alpine. Within the limits of confidence imposed by our estimates of biomass, most communities support rather similar levels of pollinator biomass; biomass is highest in the Mather chaparral (by a factor of 2x), drops by a factor of 50% in subalpine forest and San Diego coastal sage and 90% in subalpine marsh-meadow and mixed evergreen forests.

Since bee species participate in the pollination of more than 95% of the insect pollinated plants of California, it is especially important for entomologists to

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TABLE 4. Distribution of bee groups in Biotic Regions of California.
Total number of specialist-feeding bee species and number of resident plant genera associated with specialists is indicated. Total specialist bee species is highest in desert regions, though total bee species is highest in cismontane southern California. Different bee families have evolutionarily radiated to a differential extent within the different biotic realms. All numbers represent our best approximations based on the data summarized in Moldenke and Neff (1974).

Table 4.	Colletidae	Andreninae	Panurginae	Melittidae	Halictidae	Megachilidae	Anthophoridae	Apidae	Total Bee Species	Plant genera with specialist pollin.	Total specialist bee pollinators
TRANSMONTANE											
Northern Great Basin	13	30	12	0	21	72	50	15	213	17	118
Great Basin	12	18	12	0	19	66	47	5	179	14	98
Owens Valley	21	22	86	6	48	120	84	7	394	33	253
DESERT											
Mojave Desert	29	29	101	9	80	105	103	1	456	33	271
Colorado Desert	27	22	137	14	86	92	104	0	482	35	299
MONTANE											
Trinities and Siskyous	17	43	0	0	21	80	46	13	220	11	86
Alpine Sierras	15	18	4	0	25	87	20	14	183	13	89
Northern Sierras	23	70	15	0	62	137	81	10	398	28	170
Southern Sierras	20	80	25	2	96	170	116	7	516	38	219
Montane and alpine So. California	12	53	20	3	95	146	85	8	422	30	186
COASTAL											
Dunes and Sage	10	30	3	1	43	24	41	10	172	12	52
MEDITERRANEAN											
No. Coast Ranges	16	60	9	0	61	114	106	11	377	33	152
So. Coast Ranges	21	96	40	2	89	132	132	8	520	44	262
Cismontane So. California	22	98	43	7	122	119	138	7	555	47	253
Northern Central Grassland	13	48	9	0	41	45	72	10	238	29	108
Southern Central Grassland	19	84	30	1	57	54	80	7	282	36	161

document their pattern of geographical distribution. Table 4 shows that the highest diversity of bees is associated with arid and semiarid regions (data taken from Moldenke and Neff 1974). Though faunal species diversity is highest for desert regions, most species are infrequently encountered yielding the characteristic pattern of low species diversity within 0.5 km^2 areas observed in the Colorado Desert, Sonoran Desert and the Atacama (Moldenke and Neff, in press); species encountered are often in high abundance. Bee diversity is lowest along the immediate coast, the high Sierra Nevada, the rainforests of northern California and the Great Basin (the latter two regions have been very poorly collected and studied and these areas may be under-represented). Specialist coevolved bees are most abundant in desert, grassland and chaparral communities; generalists most abundant in coastal, forest and alpine communities. Table 5 records our present knowledge of the host associations and distribution of specialist pollinators (Moldenke and Neff 1974).

POLLINATION CHARACTERISTICS OF THE CALIFORNIA FLORA

Data collected from a cross-indexing of Moldenke and Neff (1974) which includes all host data on bees in California insect collections and the results of the first five years of our own community pollination research is presented in Figure 1. Plant species exhibit a wide range of success at attracting pollinators, as measured either by total number of vector species or total number of vector individuals. These data points are not robust, but they are all that is available. Relative position on the graph is undoubtedly a true portrayal for nearly all the genera listed, but the numbers are not particularly meaningful and should not be thought to indicate significant differences between plant genera located within similar portions of the curve.

FIGURE 1. Abundance and diversity of Bee Pollinators of California Plant Genera.
Figures represent a cross-indexing of all documented records of bee flower visitation presented in Moldenke and Neff (1974) and all of my own subsequent studies (Moldenke 1976 and unpublished). Numbers refer to generic designations cited in Appendix and represent the 44 most abundantly bee-pollinated genera in California. The 133 genera poorly pollinated by bees are too dendely clustered to represent separately; the symbol Ⓧ denotes several separate genera with the same abundance of vector species and individuals. Therefore, 343 genera of California are without documented native bee pollinators.

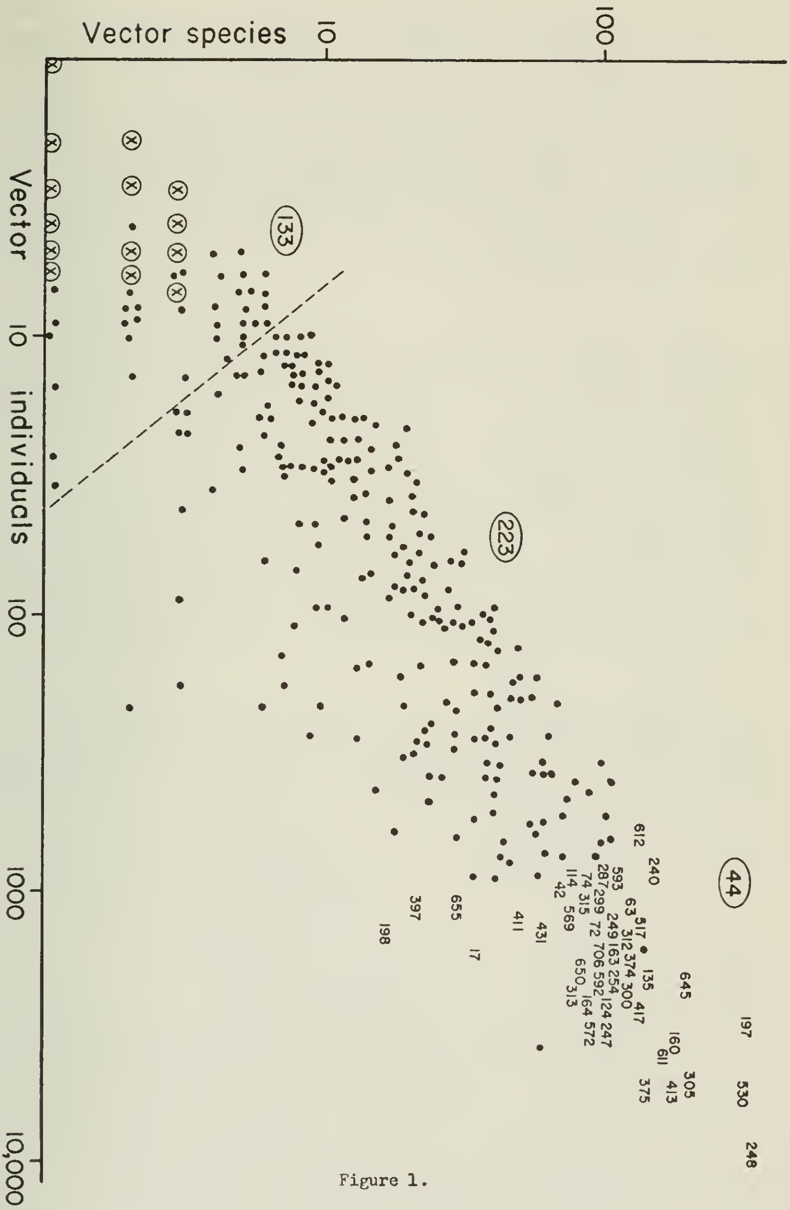
Vector species
10
100
Vector individuals
10
100
1000
10,000
133
223
44
612
240
593
287
299
114
42
74
315
569
63
249
517
312
163
374
254
300
135
72
706
592
124
650
313
164
247
572
417
645
160
611
197
305
413
530
375
248
397
655
411
431
198
17

Figure 1.

Regretably, I know of no manner in which this data can be correlated to plant abundance or relative floral biomass on a state-wide scale since no relevant censuses or reliable estimates exist. Many plants with the highest visitation rates are not abundant plants, and as such represent "cornucopia species" (e.g., Phacelia, Rhamnus, Eriodictyon, Lotus, Cirsium, Clarkia, Penstemon and Sphaeralcea). These heavily visited taxa represent less than 9% of the tabulated flora and a mere 4% of the entire entomophilous California flora; their uniqueness remains to be examined in quantitative and qualitative chemical nutritional terms.

Figure 1 demonstrates that 133 of the tabulated insect-pollinated genera are very poorly pollinated by bee taxa. More than 75% of these taxa are not pollinated by other types of pollinators and are self-compatible (or suspected of being so) and most appropriately should be treated as habitual selfers. Thus a total of about 25% of the chasmogamous nonwind-pollinated genera of California is clearly unsuccessful in competition for pollinators. Within this group of losers there are two clear components: (1) compatible taxa which compete evolutionarily by inbreeding population dynamics and short life cycles; (2) incompatible perennial taxa which can balance low visitation rates by long life cycles. This dichotomy should be apparent in the nutritional characteristics of the nectar produced.

Ten taxa display a disproportionate number of increased abundance of vector individuals relative to total vector species. The great success of relatively few taxa upon a particular floral resource implies that the resource may be difficult for generalists to utilize, but that successful exploiters are able to build up to very large populations in the absence of competition. Three of these species bloom considerably before bee diversity is apparent (e.g., Arbutus, Cynoglossum and

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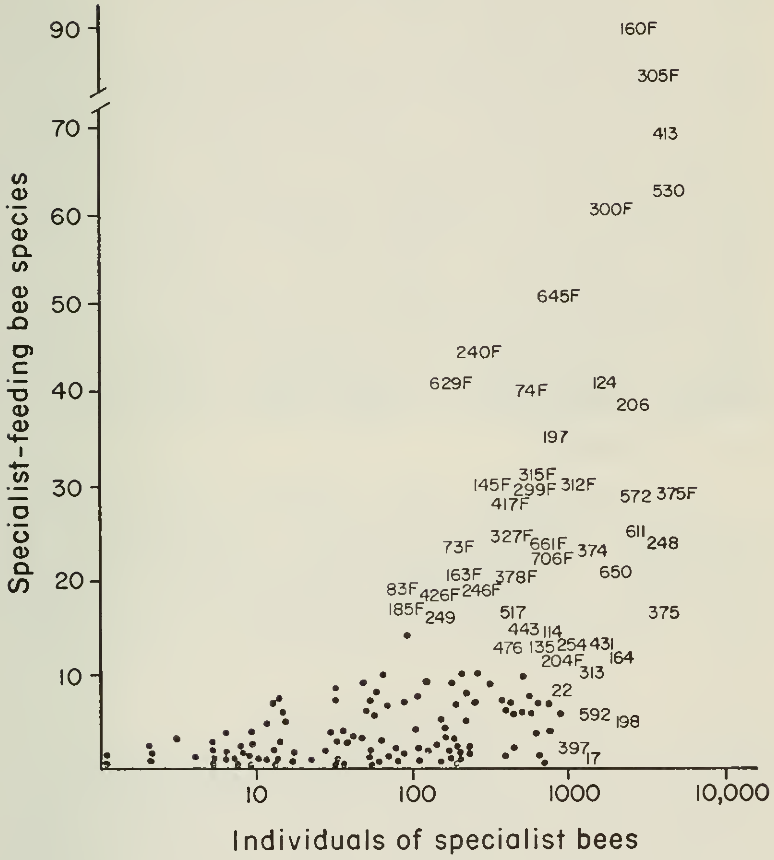
FIGURE 2. Abundance and Diversity of Specialist Bee Pollinators of California Plant Genera.
Figures represent a cross-indexing of all documented records of specialist bee flower visitation presented in Moldenke and Neff (1974) and my own subsequent studies (Moldenke 1976 and unpublished data). Numbers refer to generic designations used in the Appendix. The suffix "F" denotes the inclusion of all "Family-specific" bee visitors (in addition to those which may be generically limited) which have been documented to visit the particular genus in question. Note the extensive differences in relative abundances of specialist-feeding bees.

Figure 2.


90
70
60
50
40
30
20
10
Specialist-feeding bee species
10
100
1000
10,000
Individuals of specialist bees
160F
305F
413
530
300F
645F
240F
629F
74F
124
206
197
315F
145F
299F
312F
417F
572
375F
611
248
327F
661F
73F
374
706F
163F
378F
650
83F
426F
246F
185F
249
517
375
443
114
476
135
254
431
204F
164
313
22
592
198
397
17

Zigadenus), one genus requires special morphological adaptations for pollen collection (Coldenia) and two others bloom only in the early morning (Anisocoma and Cucurbita).

Twenty-two of the thirty-five California plant genera visited by the largest number (more than 20 species or more than 1,000 individuals with at least 10 specialist species) of specialist pollinators are composites or legumes (Figure 2). Most of the specialist pollinators of these genera are specific only to the family level, visiting any synchronously blooming species in the appropriate family. These high abundances of specialist pollinators, distributed widely throughout the entire state afford these two groups with an enormous advantage in their reproductive ecology. Character displacement of the anthesis times of congeneric sympatric plant species would be expected to evolve to facilitate greatly the efficiency of pollination systems utilizing specialist feeding bees which are seldom restricted more narrowly than the generic or subgeneric level. The other plant genera associated with large numbers of specialists are: Lasthenia, Prosopis, Larrea, Camissonia, Malacothrix, Salix, Clarkia, Eriogonum, Phacelia, Heliotropium and Sphaeralcea (Figure 2).

WIND POLLINATION

Wind pollination is the predominant mode in 18% of the California genera, most (79%) of these fall within the Graminae, Cyperaceae, Juncaceae, Gymnospermae, Amaranthaceae, Chenopodiaceae and Compositae (Ambrosiae). Only Garrya is unrelated to wind-pollinated forms in other regions and seems to be endemic to western North America; other monogeneric wind-pollinated groups are

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TABLE 5. Host-associations and Distribution of Specialist-Feeding Bees in California.
Data cited are based on the preliminary studies of Moldenke and Neff (1974). It must be recognized that they represent low estimates, for future studies will undoubtedly elucidate more instances of specialization, and many generalist-feeding taxa will be shown to have specialist-feeding geographic races which have not yet been discovered. Figures in parentheses are species which, though polylectic, heavily emphasize pollen collection from the genus in question whenever it is available. Tabular symbols * and · represent respectively the possibility of one and two additional specialist bee species, but sufficient corroborative data is lacking presently.

Table 5.	Northern Great Basin	Great Basin	Owens Valley	Mojave Desert	Colorado Desert	Trinities and Siskiyous	Alpine Sierras	Montane No. Sierras
Abronia				1	1			
Adenostoma								
Agave					1			
Amsinckia								
Arctostaphylos	1(1)	1(1)	1(1)			2(1)		3(1)
Arenaria								
Argemone			(1)	1	1			
Cactaceae			5	6	8*			
Calochortus	1	1	4*	1		1		1
Calystegia								
Camissonia	2(*)	1(*)	2(*)	17(·)	14			1
Capparidaceae			5(*)	4(*)	1(*)			
Ceanothus	1(3)	(2)	(1)			(1)		3(3)
Cercidium/Olneya				(4)	1(13)			
Clarkia	3							5
Coldenia					11			
Collinsia			1					1
Compositae	49	48	72·	67·	61*	30	26	42*
Compositae	(3)	(4)	(4)	(3)	(3)	(4)	(4)	(6)
Cordylanthus								
Cowania			1*					
Croton				1	3			
Cryptantha	2	1	7	11	6			2
Cruciferae								
Cucurbita		1	3	4	3			
Dalea			11·	9(1)*	12(2)*			
"Dandelions"	3	3	10	7	6			2
Delphinium								
Dicentra								
Dentaria								
Emmenanthe								
Eriastrum			1	1(1)	1			
Ericaceae							1	
Eriodictyon								2
Eriogonum			5	10	11			1
Eschscholzia			2	5	4(1)			
Eucnide			1					
Euphorbia				3	7			
Hackelia							(1)	
Heliotropium			1	1	1			
Jepsonia								
Larrea			8(4)	14(5)	14(4)			
Lasthenia								1
Layia								
Leguminosae	14	11	16*	12*	13	14	15	19
Leguminosae	(9)	(6)	(4)	(3)	(3)	(8)	(3)	(18)
Lepechinia								
Lepidium			1	1	1			
Lesquerella					1			
Limnanthes								1

Table 5.

	Montane So. Sierras	Montane So.California	Coastal	No. Coast Ranges	So. Coast Ranges	Cismontane So.California	No. Central Valley	So. Central Valley
Abronia								
Adenostoma	1	2(1)			2(1)	2(2)		
Agave								
Amsinckia				(1)	(1)	2	1(1)	1(1)
Arctostaphylos	4(1)	3(1)		2(1)	2(1)	2(1)		
Arenaria							1	1
Argemone								
Cactaceae			1			1		
Calochortus	3*	3		1	5	3	1	4
Calystegia	1			1	1	1	1	1
Camissonia	1	2	7	1	7	15	2	10
Capparidaceae								1
Ceanothus	5(3)	5(3)	1(2)	3(3)	3(4)	7(4)		
Cercidium/Olneya								
Clarkia	7	3		4(1)	7(1)	3(1)	2	4
Coldenia								
Collinsia	1			1	1			1
Compositae	44*	47*	14	34*	45	44	33	32
Compositae	(5)	(6)	(2)	(4)	(9)	(6)	(5)	(6)
Cordylanthus				(3)	(4)	(4)		
Cowania								
Croton								
Cryptantha	7	4		1	4	11*	2	3*
Cruciferae						1	1	2
Cucurbita						3	1	2
Dalea								
"Dandelions"	3	2		1	7	5(1)	2	6
Delphinium	1					1	1	1
Dicentra		1			1	1		
Dentaria				(1)				
Emmenanthe					2	1*		
Eriastrum					(2)			
Ericaceae								
Eriodictyon	4(1)			2(1)	4(2)	5(1)		
Eriogonum	2	2		2	4	6	1	6
Eschscholzia	3	4	1	3	6	7	2	9
Eucnide								
Euphorbia							1	2
Hackelia								
Heliotropium					2	1	1(1)	3(1)
Jepsonia	(1)							
Larrea								
Lasthenia		1	3	2	6	7	9	9
Layia		1	1			4	2	2
Leguminosae	26	27*	5	18	24*	17	11	13
Leguminosae	(17)	(17)	(5)	(7)	(19)	(17)	(4)	(6)
Lepechinia					1	1		
Lepidium								
Lesquerella								
Limnanthes	1				1	1	1	1

Table 5.

	Northern Great Basin	Great Basin	Owens Valley	Mojave Desert	Colorado Desert	Trinities and Siskiyous	Alpine Sierras	Montane No. Sierras
Linanthus	1			1	1			3
Lycium					2			
Malacothamnus								1
Meconella								
Melilotus								
Mentzelia			3*	6*	8(1)			
Mertensia		1					1	
Mimulus	1		1					2
Monardella								
Nama			1	5	6			
Nemophila								2
Orthocarpus								
Penstemon	2*	1	5			2(1)	6	4(1)
Perideridia								
Petalonyx				1	1			
Phacelia	6	7	16*	17	15	6	9*	11
Phacelia	(1)	(1)	(1)			(2)	(4)	(3)
Physalis				1	2			
Platystemon								
Proboscidea				1	1			
Prosopis			12(2)	15(2)	23(3)			
Potentilla			2				5	2
Psoralea								
Ranunculus						5	1	4
Rhamnus								
Ribes								1
Rosaceae	1					1	2	1(2)
Salix	5*	4	3	3	3	7	3	8
Salvia			1					
Sidalcea								1
Sphaeralcea			12	14*	17*			
Stachys								
Stephanomeria				2	3			
Symphoricarpos	1	1	1					
Trichostema								
Trifolium	3	2	2	1			3	4
Umbelliferae						1	1	2
Zigadenus								

Table 5.	Montane So. Sierras	Montane So. California	Coastal	No. Coast Ranges	So. Coast Ranges	Cismontane So. California	No. Central Valley	So. Central Valley
Linanthus	3	2		2	2	6*	1	1
Lycium								
Malacothamnus	2	2		1	3	2	1	2
Meconella					1			
Melilotus								1
Mentzelia								
Mertensia								
Mimulus	4				1			
Monardella	1	2			1	1		
Nama								
Nemophila	4	6		3	5	3	3	3
Orthocarpus					(1)		(1)	(1)
Penstemon	6(1)	6(1)		1(1)	2(1)	1		
Perideridia	1							
Petalonyx								
Phacelia	18*	12	3	11	17	18*	7	10
Phacelia	(2)	(2)		(1)	(4)	(2)		(1)
Physalis								
Platystemon					6	3*		
Proboscidea								
Prosopis								
Potentilla	3	2						
Psoralea					1			
Ranunculus	3	3	2(1)	4	3	2	2	2
Rhamnus		2			2	3		
Ribes	1	1*		1				
Rosaceae	1(2)	1		(1)	(1)			
Salix	8	5		6	7	8	2	5*
Salvia					1	1		
Sidalcea	2			1	2	2		
Sphaeralcea								
Stachys				(1)	(1)	(1)		
Stephanomeria	1	1			2	2		1
Symphoricarpos								
Trichostema	(1)			(1)	(1)	(1)		
Trifolium	4	1		3	3	2	2	2
Umbelliferae	1			3	2	2	2	3
Zigadenus	2				2		1	2

either widespread in adjacent regions or relicts of formerly much wider distribution (e.g., Empetrum, Forestiera, Simmondsia, Thalictrum, Batis, Oligomeris, Eremocarpus, Tetracoccus, Datisca).

Wind pollination is the dominant form of pollination in all California forest and grassland communities. In these communities the dominant plants, with the largest relative biomass of flowers, are all wind-pollinated. Species composition of communities reveals a low of 10% wind pollination in chaparral ecosystems (generally confined to the herb stratum), to a high of 35% in the subalpine marsh-meadow, with most communities averaging about 15%-22% anemophily in the flora. An average of 27% of the flora at subalpine and alpine localities is wind-pollinated; this percentage drops to 18% at altitudes of 1,300 m and sea level as the general abundance of insect pollinators increases.

WATER POLLINATION

The only documented examples of water pollination in the California flora that I am aware of involve species in the Zosteraceae, Zannichelliaceae, Ruppiaceae and Najadaceae. In all cases, except for Ruppia, water pollination is associated with unisexual flowers. These are all very widely distributed plant genera and their pollination adaptations (Faegri and van der Pijl 1966) are not unique to our region.

HABITUAL SELFING

Eighteen percent of the genera of angiosperms in California are habitual or obligate selfers (not counting any "wind-pollinated" selfers). Most of these genera are in families composed predominantly of small annual plants, many of which are habitual selfers (e.g., Cruciferae, Caryophyllaceae, Boraginaceae, Portulacaceae, Compositae [Inulae]). A large percentage of them are endemic to California and adjacent regions and presumably evolved locally; this particular method of estimating the endemicity of selfing taxa yields a low estimate, since many normally chasmogamous genera have evolved individual selfing species on numerous occasions in California (e.g., Astragalus gambellianus, Lupinus micranthus, Lotus micranthus). Predominantly selfing genera that have speciated the most noticeably in California are those which are visited occasionally by pollinators (e.g., Cryptantha spp., Eriogonum spp.). Inbreeding population dynamics of themselves does not seem to have noticeably increased evolutionary rate within the California flora though many of the most diverse genera are genetically compatible (e.g., Mimulus, Gilia s. lato, Potentilla); all of these genera are frequently cross-pollinated.

Habitual selfers are most abundant in grassland communities (41%-42% of the flora at Stanford and Camp Mather--Table 2). Relatively high levels of habitual selfing are also found in the annual forbs of the immediate coast (ca. 30% of flora); the subalpine talus (35%), the desert annuals (38%) and the arctic-alpine (39%). Obligate selfing constitutes approximately 5% or less of the flora in all communities, except for high levels in the serpentine grasslands (18%), coastal sage (9%-11%) and subalpine talus (8%). High levels of selfing and obligate selfing are found, of course, in both the weedy and offshore island communities. Habitual and obligate selfing is correlated to annual habit and often associated with climatic conditions under which pollinators are either consistently lacking or periodically in very low abundance. In grasslands, where pollinators are often abundant, obligate selfers are species which bloom before the period of activity of the pollinators. At Jasper Ridge, pollinator diversity and biomass starts to rise noticeably during the first week of April; by this time 68% of the 27 obligate selfers have already nearly finished blooming. The selective pressures forcing such an early period of anthesis upon so many unrelated plants must remain speculative.

BEE POLLINATION

Of all the forms of animal vectored pollination, pollination by bees is the most significant in all communities based upon the percentage of the flora so dependent (Table 2; Appendix). Bees visit nearly every type of nonwind-pollinated flower morphology, excluding perhaps only some of the more highly modified hummingbird, moth and fly forms. Bees may function as locally important pollinators to seldom-visited plant species because of the plumose pubescence (to which pollen readily adheres) and their strong behavioral tendency to visit the same plant species on subsequent visits. The most generalized opportunistic bee feeders (bumblebees in forest, coastal and alpine communities; halictines in Mediterranean climates and open forest understory) are undoubtedly the most significant outcrossers of plant species in very low abundance or locally common species with inconspicuous flowers and rather low reward levels per flower. These generalist bees function as the most significant pollination element in California, since in addition to their pollen vectoring for the 86% of the genera on which other vector agencies have not been recorded in Table 1, they efficiently service nearly all the angiosperm genera frequently visited by other sorts of pollinators (including specialized solitary bees). The percentage of the flora they service in any community is a close approximation to the total flora minus the wind-pollinated forms and obligate selfers. Both bumble and halictine bees are extremely significant in the pollination of introduced weedy plants, since the new introductions are either ignored by the native pollinator fauna in native surroundings or all other groups of pollinators from heavily disturbed situations.

Halictine bees serve as the primary or sole vector for a rather small percentage of the flora (ca. 5%) in all but the chaparral, talus scrub and grassland communities where they assume a much more significant role (ca. 15%). In the subalpine marsh-meadow and desert communities they are seldom the principal vectoring agency for any plants whatsoever. Bumblebees serve as the primary or sole pollinating agency for a much more variable percentage within differing plant communities. They are nearly absent from San Diego County and the desert regions and do not function as exclusive vectors for any plant species whatever. In coastal, montane, alpine or dense forests the percentage of the flora served primarily by their agency rises generally to more than 20% (a high of 47% in coastal communities).

Solitary bees as a group are the most interesting. Time and time again, coevolutionary relationships have been established between specialist-feeding bees and particular host plants. Community analyses have shown (Table 2) that solitary bees are a primary pollinator for an average of 12% of the flora at Point Reyes, 20% at Tioga Pass, 34% along the San Diego County transect, 42% at Stanford University (excluding deep forest), and 51% at Camp Mather (excluding forest). The percentage of plants serviced by specialist solitary bees follows similar overall site trends but is characterized by a noticeable drop in all forest communities and a peak in chaparral scrub and desert communities. It is a frequent occurrence to observe several species of obligately specialized bees on local populations pollinated exclusively by their agency.

BEEFLY POLLINATION

Beeflies (Bombyliidae) serve as the primary pollinator for 10%-20% of the resident flora in low to middle elevation central California community types; they are insignificant elements in the alpine communities and drop in relative importance (though not abundance) in the communities of southern California. The Compositae (associated with the short-tongued genera Anthrax, Conophorus, Conophanus, Exoprosopa, Poecilanthrax and Villa) and the Boraginaceae and Polemoniaceae (associated with the long-tongued genera Bombylius, and the smaller-bodied Oligodranes, Geron, Phthiria) are often intimately associated in close coevolutionary patterns (Grant and Grant 1965). Many of these insects are inquiline parasites on solitary bees as larvae and will be found primarily in regions of large solitary bee abundance; the smaller species are often parasites of grasshopper egg cases. Long-tongued beeflies often hover in front of the flower while feeding and, as such, pollen transfer must be limited to pollen adhering to the proboscis (e.g., Cryptantha). Many members of the Polemoniaceae have strongly exerted anthers and stigmas which contact the hovering insects as they probe the long tubes for nectar. Though many species are "apparently" morphologically adapted for sipping nectar only, most species are suspected of being major pollen consumers as well (A. Moldenke, J. Neff, J. Hall, unpub. observations).

Seventy-three genera of California plants are frequented by beeflies and the closely related spider predators, the Acroceridae (Cyrtidae). Acrocerids have immense non-retractile slender proboscises, sometimes nearly twice the length of the body. Acrocerids are often the major or sole pollinators of Azalea, Brodiaea, Calystegia, Diplacus, Iris and Monardella populations; they also frequent Clarkia, Cryptantha, Eriogonum, Linanthus, Penstemon, Salvia and Wyethia in significant numbers along with other pollinator groups as well. Bombylius major is a species associated with forest understory communities and exerts a major role in the pollination of 20 genera of plants in these localities and along the immediate coast as well (e.g., Arbutus, Arctostaphylos, Cakile, Collomia, Cynoglossum, Dentaria, Fragaria, Hackelia, Lithophragma, Smilacina, Solanum and Viola). Other species of the genus, and B. major to a lesser extent, are the major pollinators of grassland and desert Polemoniaceae, Boraginaceae, Centaurium and Petalonyx. Of the many genera of fall composites heavily visited by the generally short-tongued Tomophthalmae, all are visited by numerous other vectors as well. Even though visited by numerous solitary bees, Lasthenia is so heavily visited by the genera Conophanus and Conophorus that they must play a very significant role in its reproductive ecology. Few plant genera are obligately dependent upon the vectoring afforded by the tiny Phthiriinae, Gerontinae and Usiinae; Allophyllum, Calycoseris, Kelloggia and Nemacladus are the most closely tied. All of the non-forest genera relying upon beefly pollination are genetically compatible and capable of selfing in their absence.

HOVERFLY POLLINATION

Less than 5% of the flora within all the California communities we studied relies upon the exclusive pollination of hoverflies (Syrphidae). All of these taxa are small-flowered annual plant species which would self in the absence of hoverflies and may be outcrossed most frequently by halictine bees at other sites. No instances of close coevolutionary relations between California plants and hoverflies are known to me. In the weedy community, the tiny hoverflies (Paragus, Allograpta) visit many nearly cleistogamous species and may play a significant role in the genetic recombination of these weed species; syrphids seldom have much facial pubescence and hence may not vector pollen as frequently as their abundance upon flowers might indicate.

"FLY" POLLINATION

Various other fly groups assume importance only in rare circumstances. Anthomyiid pollination is pronounced only in subalpine regions (16% of the forest and marsh-meadow flora necessitating their vectoring, 8% of the talus community). Flesh-fly pollination has evolved with Scoliopus and is reported for Bebbia, but I doubt its general significance in the latter case. Bebbia may be found in bloom nearly 12 months of the year; usually it is heavily visited by butterflies and composite-associated solitary bees. Coelopid fly pollination is an unstudied possibility in estuarine marshes and offshore islands, presumably no plant not normally self-pollinating relies heavily upon their visitation. Mycetophilid pollination is known only in the Aristolochiaceae in California (Vogel 1973); since this is the general pattern for the family, little special coevolutionary adaptation apparently has occurred in California. Mosquitos (particularly males) are extremely inefficient pollen vectors, but may exert an outcrossing effect for the normally self-pollinated genera, Habenaria and Sambucus; in more northerly distributions of these taxa, the vectoring by mosquitos becomes much more frequent (i.e., Stoutamire 1970). Heuchera and Arceuthobium (Stevens and Hawksworth 1970) rely exclusively on gnat pollination; these adaptations also are ancient adaptations and not uniquely characteristic of the California flora.

WASP POLLINATION

Forty genera of plants in California are frequently visited by sphecoid and vespoid wasps although only 24 are visited consistently, regardless of local circumstances.[d] Plant species relying heavily upon wasp pollination are infrequent throughout California (less than 3% of the resident flora locally, reaching highest levels in chaparral and desert communities [ca. 5%]). The importance of wasps in the pollination of Cryptantha and Eriogonum depends upon the local abundance of more efficient pollen vectors, but Antennaria, Gnaphalium Cuscuta, Achillea and Baccharis are generally heavily outcrossed by their agency. Scoliid wasps (e.g., Campsomeris) are important pollinators of Mesembryanthemum chilensis both in California and Chile. Asclepias is primarily pollinated by large tarantula-hawks (Pompilidae), especially in more southerly locations. The related mimosoid genera Prosopis and Acacia are heavily visited by diverse wasp groups; the latter is primarily wasp pollinated, whereas the former is a cornucopia exploited by many groups of pollinators. Wasps are never associated with papilionaceous flowers except for Maricopodynerus which is a specialist on Dalea (R. Snelling pers. comm.). The extremely abundant social wasps of the tropics (i.e., Mischocyttarus) which visit flowers in enormous abundances are not found associated with flowers in California.

Only the masarid wasps (Pseudomasaris spp.) utilize floral resources as the sole provision for the young in a dependency closely analogous to bees. Pseudomasaris vespoides is specific to Penstemon, while the other species frequent specifically Phacelia and Eriodictyon. Though the flora may not have coevolved with a reciprocal dependency, this diverse genus is distributed only in Madro-Tertiary regions of western North America (Torchio 1975).

The primitive sawflies (Tenthredinidae) are important pollinators of Nemophila, Phacelia, Polygonum bistortoides, Salix, Sambucus and Valeriana. Except for the hydrophyllaceous genera, these genera are closely associated with sawfly pollination throughout alpine western North America.

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[d] Consistently visited taxa: Acacia, Achillea, Asclepias, Baccharis, Chrysothamnus, Cryptantha, Cuscuta, Encelia, Eriodictyon, Eriogonum, Eriophyllum, Euphorbia, Haplopappus, Helianthus, Lepidospartum, Perideridia, Prosopis, Salix, Solidago, Sphenosciadium, Vigueria, Wislizenia.

BEETLE POLLINATION

Beetle pollination is a poorly studied and diverse phenomenon. Nearly all species of California plants in which beetles play a significant role in pollination are visited by additional vector types as well (see Appendix). Hence, no specific morphological floral adaptations for beetles has evolved. Tumbling flower beetles (Mordellidae) are very important pollinators of the Umbelliferae and mass-blooming Rosaceae. Long-horned wood-borers (Cerambycidae) are important pollinators of *Ceanothus*, *Ranunculus*, the Melanthaceae, *Sambucus*, *Achillea*, and other tight inflorescences of small white flowers. Metallic wood-borers (Buprestidae) are important pollinators of yellow flowers or inflorescences in the early spring (i.e., *Ranunculus*, *Camissonia*, *Eriophyllum*, *Wyethia*). Many other beetle groups commonly found on flowers probably cause more destruction by their feeding than their use as vectors can compensate (i.e., Meloidae, Dermestidae, Chrysomelidae). I have consistently been unable to find evidence of beetle pollination in *Paeonia* and *Calycanthus* (Grant 1950); the former is a heavy selfer facultatively outcrossed under most circumstances by solitary bees of the genus *Andrena*.

BUTTERFLY POLLINATION

Plants that have coevolved specifically for pollination by butterflies are rare in the California flora (see Appendix). *Verbena* (*Glandularia*) and *Phlox* are widespread groups dependent upon butterfly pollination throughout their range. Most genera of the Compositae are pollinated by butterflies as well as many other groups of vector taxa. Abundant individuals of *Danaus*, *Colias* and *Pieris* are important pollinators of their host plants (Asclepiadaceae, Cruciferae, Capparidaceae, and Leguminosae). Butterfly pollination is most frequent in open chaparral and grassland communities. In alpine ecosystems many moths, unable to fly under the prevailing cold nighttime conditions, visit inflorescences primarily of the Compositae during the daytime. At lower elevations, the moth genera *Adela* and *Schinia* are abundant daytime pollinators in grassland and open forest habitats. A catalogue of published butterfly floral visitation records is available (Shields 1972), but since the catalogue does not distinguish between rare instances of visitation and consistent fidelity to a plant group, the information is difficult to interpret.

MOTH POLLINATION

Moth pollination (except for sphinx pollination, which is more properly treated below) is poorly studied and little developed in California. Moths visit the flowers of many white-flowered plants at night; however, most of them have already been fully pollinated during the day. With the exception of some species of Phlox, Silene, Gaura, Madia, and Chlorogalum, I suspect that noctuid or geometrid pollination is insignificant for California plants. The remarkable coevolutionary relations between moths and Yucca discovered by Riley (1892) and reviewed in detail by Powell and Mackie (1966) are unique to western North America. Gaura and Clarkia breweri (MacSwain et al. 1973) are onagraceous plants which are usually moth-pollinated; the former is widely distributed throughout arid North America. Madia elegans and Chlorogalum pomeridianum are species which open in the late afternoon presumably as a response to selection for moth pollination; these species are frequently heavily visited by bees prior to darkness, at which time the moths become active.

SPHINX AND HUMMINGBIRD POLLINATION

A more frequent and closer dependency is exhibited between sphinx moths and native plants. Ten genera have coevolved with these high-energy requiring facultatively homeothermic pollinators (e.g., Aesculus, Abronia, Aquilegia, Azalea, Chlorogalum, Datura, Hesperocallis, Mirabilis, Nicotiana, Oenothera)although sphinx moths are pollinators for many other genera as well. Species in the genera Aesculus,Aquilegia, and Azalea have been documented to utilize sphinx moths to transfer pollen only in the western United States, and presumably this trait is locally evolved, as in the case for Abronia (Tillett 1967), Chlorogalum and Hesperocallis, which are endemic to arid or semiarid western U.S.A. in many localities, sphinx moths are active during the day; they closely resemble hummingbirds and indeed visit many of the same plant species.

Thirty-nine genera are pollinated by hummingbirds and have evolved extensive morphological adaptations to effectively exclude other types of pollinators and produce better visibility to the hummingbirds.[e] Hummingbirds are important pollinators of many less specialized genera as well: *Agastache*, *Arbutus*, *Arctostaphylos*, *Cirsium*, *Dicentra*, *Dudleya*, *Eriodictyon*, *Erysimum*, and *Xylococcus*. In all communities hummingbird pollination is confined to only several (usually less than 10) plant species, which typically exhibit protracted anthesis periods. Too much emphasis has been placed on the difference in pollination by sphinx moths and hummingbirds; both are high-energy-requiring facultative homeotherms and both tend to visit the same species of plants (often contemporaneously). A critical paper by Watt *et al*. (1974) demonstrated conclusively that the floral adaptation to both pollinators was similar. Plants supporting these pollinators usually produce voluminous nectar of complex rather than monomeric sugars; these nectars, therefore, contain increased energy at the concentrations characteristic of most other plants. Evolutionarily the increased specificity and distance of pollen transport has evidently been worth the added energetic cost to the plant. Important studies on hummingbird pollination in California have included those of Pearson (1954), Grant and Grant (1968), Hainsworth *et al*. (1972) and Stiles (1973).

SUMMARY

Synecological analyses of pollination ecology have been initiated only recently. Nevertheless, studies have shown conclusively that in some vegetation types (e.g., alpine tundra, subalpine marsh-meadow, subalpine forest, northern coastal shrub, coastal sage, maritimal dunes, redwood forest, and mixed evergreen forest) most plant species are pollinator limited and must compete for visitation by vectors which are generalist feeders and must be supplied with a sufficient reward to ensure subsequent visits to the same plant species. In chaparral, valley grassland, warm desert, weed, and open forest communities, pollinators are usually very abundant and

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[e] *Aconitum*, *Agave*, *Antirrhinum*, *Aquilegia*, *Astragalus*(?) (Grant and Grant 1968), *Beloperone*, *Brodiaea*, *Castilleja*, *Chamaenerion*, *Chilopsis*, *Cleome*, *Cleomella*, *Collomia* (?) (Garnt and Grant 1968), *Delphinium*, *Fouquieria*, *Fritillaria* (?)(Grant and Grant 1968), *Galvesia*, *Gilia* (*Ipomopsis*), *Iris*, *Isomeris*, *Lepechinia*, *Lilium*, *Lobelia*, *Lonicera*, *Lycium*, *Mimulus*, *Mirabilis*, *Monardella*, *Pedicularis*, *Penstemon*, *Ribes*, *Ruellia*, *Salazaria*, *Salvia*, *Scutellaria*, *Silene*, *Teucrium*, *Trichostema*, *Zauschneria*.

flower visitation is assured; specialist pollinators are abundant in these environments. However, those perennial plants that require outcrossing still must rely upon large-bodied, far-ranging generalist pollinators to achieve efficient interplant pollen flow.

Though many of the interrelations between plants and their pollinators have now been tentatively delineated, we know little of the ecological and evolutionary significance of different modes of pollination. Unquestionably, valid representations can be made of community-wide phenomena as as they occur in various localities throughout the state. It must be remembered, however, that the pollination of any one particular plant species is subject to considerable variability depending upon circumstance. Since the energetic and nutritive reward of the floral attractants is genetically determined and not subject to modification by the immediate competitive environment of a plant individual, competition patterns for vectors may have considerably different outcomes locally; some cornucopia species may be barren of vectors and some habitually selfed species may be heavily outcrossed. Knowledge of the patterns of pollination interactions within differing vegetation types now permits us to assess the roles of these pollination syndromes in the evolution of our native plant communities.

ACKNOWLEDGEMENTS

I would like to thank especially my colleagues John Neff and Patricia Lincoln for their assistance in cataloguing the data on museum specimens, their valuable collections and field observations on pollination ecology and their critical reading of the manuscript. Alison Feerick M. read and criticized the manuscript extensively. This paper was prepared in part in response to interest expressed by Michael Barbour and Jack Major and their excellent editorial comments are sincerely appreciated. These studies were originally undertaken under the guidance of Peter Raven and more recently have been generously subsidized by the Origin and Structure of Ecosystems Program of the International Biological Program.

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APPENDIX

POLLINATORS AND BREEDING SYSTEMS OF THE ENTOMOPHILOUS AND ORNITHOPHILOUS PLANTS OF CALIFORNIA

Three hundred genera of the California flora are cited below associated with their documented major pollinators. Where known, an estimate is made of the effectiveness of their outcrossing and whether or not selfing is possible as well. Anemophilous genera, habitually selfed genera, and genera about which I have no first-hand knowledge are omitted. Genera are presented alphabetically and the number which precedes them is cited in the previous figures.

The first column represents the results of bagging and greenhouse transplantation studies. G=genetically self-compatible; I=self-incompatible; A=apomictic. If genetically self-compatible, the number which follows is my rough estimate of the degree of outcrossing usually encountered in native populations of species of this genus. (1=habitually selfed; 5=nearly always very heavily outcrossed.) If self-incompatible, the number represents the usual level of seed-set encountered in wild populations and the general abundance of pollinators observed on the flowers. (1=seldom visited, seed-set very low; 5=heavy visitation and full seed-set). "I" indicates strong mechanical or temporal barriers to inbreeding even though the flowers are genetically self-compatible to my knowledge.

The second column indicates the major pollinators (not simply visitors) of the genus. Especially important groups are denoted by "!". BBY=Bombyliidae, B=_Bombylius_, O=tiny species such as Oligodranes and Phthiria, V=short-tongued groups such as many Villa, A=the closely related Acroceridae; MUSC=Muscoidea; PFLY=primitive Diptera such as gnats and mosquitos; SYR=Syrphidae; TACH=Tachinidae; TEPH=Tephritidae; WASP=Sphecidae and Vespidae; MASAR=Pseudomasaris (Masaridae); PWSP= Ichneumonoidea; SAWF=sawflies (Tenthredinidae); BEET= beetles (Coleoptera), BP=Buprestidae, CC=Coccinellidae, CR=Chrysomelidae, CY=Cerambycidae, D=Dermestidae, MD= Mordellidae, ME=Melyridae, ML=Meloidae, EL=Elateridae, NT=Nitidulidae; BUTT=butterfly; MOTH=non-sphyngid moth.

The third column represents the known important bee pollinators of the respective genus (occasional visitors are not cited, only those frequent and widespread enough to act as significant factors in the pollination ecology of the genus). Collective designations are employed where possible: CMP=the guild of Compositae-specific bees of diverse families; HAL= the guild of "table-scrapping", sometimes colonial, Halictinae which are generalist feeders usually; PLY= an even more inclusive category of generalist feeding bees, including many genera in all families and many species of bees whose males may be common generalists even though the females are restricted to one genus of plants.

UNDERLINING signifies that the cited genus contains one or more species restricted to, or heavily emphasizing, pollen-collection from this plant genus throughout large geographic areas. AG=Agapostemon, AD=Andrena, ANT=Anthidium, AN=Anthophora, AS=Ashmeadiella, AT= Anthocopa, AU=Augochlorella, BB=Bombus, CH=Chelostomoides, CL=Chelostoma, CN=Centris, CO=Conanthalictus, CR=Ceratina, CT=Colletes, DD=Diadasia, DI=Dialictus, DN=Dianthidium, DF=Dufourea, EM=Emphoropsis, EV=Evylaeus, EX=Exomalopsis, HM=Hypomacrotera, HP=Hoplitis, HS=Hesperapis, HY=Hylaeus, HT=Heteranthidium, ID=Idiomelissodes, LS=Lasioglossum, LT=Lithurge, MG=Megachile, ML=Melissodes, ND=Nomadopsis, NM=Nomada, NO=Nomia, OS=Osmia, PN=Panurginus, PP=Peponapis, PR=Perdita, PRT=Proteriades, PT=Protodufourea, SP=Sphecodes, SY=Synhalonia, TP=Triepeolus, XG=Xenoglossodes, XN= Xenoglossa, XR=Xeralictus, XY=Xylocopa, Θ signifies groups conspicuous in their absence, as we presently understand the occurrence of pollinators.

1	Abronia	?I/G-1	SPHINX	AN,BB
3	Acacia	I-4	WASPS!	PR,CT,CH
6	Acamptopappus	?G	BBY	CMP!PLY(DI)
8	Acer	I-5/G-2	wind,PWSP	BB!
9	Achillea	I-3	BEET!(CY,D,MD, CC)SYR!MUSC!WASP!	PLY(HY!LS!EV,SP) Θ(CMP,BB)
14	Aconitum	G,A-5	BIRD!	BB!
17	Adenostoma	I-3	BEET!(CC,D),WASP, BUGS,MOTHS	HAL!(AG,AU),PR, HS
19	Aesculus	G-5	BUTT!SPHINX!MOTH	EV
20	Agastache	?-5	BIRD	BB!XY!AN!
21	Agave	I-5	BIRD!	PR,XY
22	Agoseris	I-?	BEET(BP),SYR	AD!AD!PR!HAL! Θ(CMP)
28	Allium	G-3	BBY(B),BIRD	BB!CH,OS,HP, DI,NM
29	Allophyllum	G-2	BBY(O)	---
36	Amelanchier	I-2	SYR	AD!
40	Amorpha	?-5	BUTT!	CT!PLY
42	Amsinckia	G/I-1/5	BBY!(B,O),BUTT	AN!OS!SY!BB! EM!ML
45	Anaphalis	?"I"	BEET(MD!)	PLY,Θ(CMP)
50	Angelica	?	BEET(MD!)	PLY(HY,DI)
51	Anisocoma	?	BBY	AN!KD!PLY(DI,AG) Θ(CMP)
52	Antennaria	?"I",A-1	PWSP,BUTT,MUSC, WSP!	Θ(CMP)
53	Antirrhinum	G-1/5	BIRD!	PLY
56	Apocynum	?	WASP!BUTT!	PLY(HY!DI)
57	Aquilegia	G-5	BIRD!SPHINX!	BB!
58	Arabis	G-1	SYR	PLY
60	Arbutus	I-2/5	BBY(B),BIRD	BB!EM!OS!
61	Arceuthobium	I-?	GNATS	---
63	Arctostaphylos	I-5	BBY(B,O),MUSC, BIRD	BB!AD!AD!EM!SY! OS!HAL,NM
64	Arenaria	G-2	WASP,SYR	HAL,AD
65	Argemone	?	BEET(ML)	HAL!PR,AD
66	Aristolochia	I-?	MYCETOPHILIDS	---
68	Arnica	G,I,A-1	BUTT	BB,Θ(CMP)
71	Asarum	?	MYCETOPHILIDS	---
72	Asclepias	I-5	BUTT,WASP,BEET(MD)	PLY(HY,DI),XY!BB, MG,ML
73	Aster	(G)I-1/5	BUTT,MUSC,BBY(V,B)	CMP!HAL!
74	Astragalus	I,G-1/5	BUTT,BIRD?	AT!ANT!OS!SY!BB! HP!

79	*Baccharis*	I-1/5	BEET!(MD),WASP! MUSC!PWSP	DI!HY!PR,BB!Θ(CMP)
82	*Baileya*	?	BBY(V)	CMP!(PR,ML),PLY!
83	*Balsamorhiza*	?I-5	BUTT	CMP!BB
84	*Barbarea*	±I-3	BUTT!	AD,PLY
86	*Bebbia*	?	MUSC!BBY(V,O)	CMP!Θ(HAL)
87	*Beloperone*	?I	BIRD!	AN
89	*Berberis*	I-1/5	---	BB!AD
95	*Blennosperma*	G-?	---	AD!AD
99	*Boerhaavia*	?	MUSC,TIPHIIDS	EXO,HAL
100	*Boisduvallia*	G-2	BBY(V)	---
108	*Brodiaea*	I-3/5	BEET(CY,ME,D),SYR BBY(A,B),BIRD?	BB!SY!HAL!OS!
112	*Calandrinia*	G-3	---	AD,HAL
113	*Calliandra*	I-1	---	DI
114	*Calochortus*	G-5	BEET(CY,ME,MD,D, BP),+++	PR!ND!DF!++
118	*Calycadenia*	?	BBY(O,V),PWSP, BEET(ME,ML),++	CMP!HAL!
119	*Calyptridium*	G-1/5	BUTT,WASP,BEET(ML)	PLY
120	*Calycoseris*	?G	BBY!(O),BEET(ML)	ND,PR,PLY
122	*Calystegia*	?	BBY(A)	DD!CR,PLY(HAL)
124	*Camissonia*	G/I-1/4	---	AD!DF!HAL,PLY,+
131	*Cassiope*	I-5	---	BB!AD
132	*Castilleja*	I/G-2/5	BIRD!	BB!AN,OS
135	*Ceanothus*	I-5	PFLY,MUSC,SYR, BBY(O),BEET(CY! D,ME,CC,EL)	AD!AD!PN!HAL! BB!HY
137	*Centaurium*	G-2/3	BBY(B)	HAL,CR
141	*Cercidium*	I-5	---	CN!AS,CH,CT,PR
142	*Cercis*	I-5	---	XYL!BB
143	*Cercocarpus*	G-3	---	BB,AN.EM,DI,EV
145	*Chaenactis*	G-1	BEET(ME!),BBY! (O,B,V)	CMP!HS,Θ(BB)
147	*Chaetopappa*	?G-4	BBY(V!),BUTT	AS,DS,PLY Θ(BB,MG,ML)
148	*Chamaebatia*	?-2/5	BUTT!WASP,BBY(V) BEET(D,MD)	AD!ND!HAL!OS! HP,PLY
151	*Chamaenerion*	"I"-5	BIRD,SPHINX	BB!PLY
153	*Chilopsis*	?I-5	BIRD	PLY!XY!CN!AN,MG
155	*Chlorogalum*	G-5	SPHINX,MOTH,WASP	BB!HAL
156	*Chorizanthe*	G-1	WASP,BBY(O)	PLY
158	*Chrysopsis*	I-4	BUTT!	CMP!BB!HAL!
160	*Chrysothamnus*	I-5	BUTT!WASP!+++	CMP!(AD!CT!MG! ML!PR!),PLY!BB!++

163	*Cirsium*	I-5	BIRD!BUTT!BEET (ME)	OS!CMP!(OS,MG, DN),BB!HAL!SY!PL
164	*Clarkia*	G-2/5	BIRD?MOTH,BEET (M,BP,CY),BBY (B,O,V,A)	HS!MG!AD!OS,HAL (EV,DI),CR++
166	*Clematis*	G/I-1	SYR,BBY	BB,AD,NM,PLY
167	*Cleome*	?	BUTT!BIRD!	BB,PLY,ND
168	*Cleomella*	?	BIRD?BUTT	BB!HAL!PLY,PR,ND
171	*Coldenia*	?G-2	---	PR!
173	*Collinsia*	G-2/5	---	OS!HP!AT!Θ(BB,HA
174	*Collomia*	?G-1/5	BBY(B),MOTH,BIRD?	---
184	*Cordylanthus*	?-4	WASP,BBY(O,V)	CH!ANT!AS,MG
185	*Coreopsis*	?-5	SYR,BUTT?	CMP!OS!HAL,AD, SY,TP
186	*Corethrogyne*	?I-5	BUTT,BBY(V)	CMP!(ΘMG,ML),HAL PLY
187	*Cornus*	?-1	BEET(CY)	---
190	*Cowania*	?	BEET(MD,D)	PR,PR,PLY,HAL,AD
192	*Crepis*	I,G,A-?	SYR,BEET(BP!), BUTT	AD!HAL!
196	*Croton*	?	WASPS!	HAL!PR,MG,ML,PLY
197	*Cryptantha*	G-1/3	BBY(B,O,A)! WASP!TACH	AD,PRT + all groups
198	*Cucurbita*	I-5	---	PP!XN!AG
199	*Cuscuta*	G-1/3	WASP!	PLY
202	*Cymopterus*	?	BBY,WASP,SYR	DI!
204	*Cynoglossum*	I-3/4	BBY!(B)	AN!
206	*Dalea*	G/I-1/5	WASP	AT!ANT!AS!PR!OS! PR,PLY
209	*Datura*	?	SPHINX	HAL!PLY
211	*Delphinium*	G-4/5	BIRD!	BB!SY
212	*Dendromecon*	?-2	SYR	PLY
213	*Dentaria*	I-2	BBY!(B),SYR	AD!
214	*Descurainia*	G-3	SYR	AD,HAL
215	*Dicentra*	?	BIRD	CH!XY!OS
223	*Dodecatheon*	G-2	---	BB
225	*Draba*	G-1	SYR	HAL
228	*Dudleya*	G-5	BIRD	BB!AN!
233	*Echinocactus*	?	---	DD!AS,LT!DI
234	*Echinocereus*	?	BEET(NT),BIRD?	DD!AS,LT!PLY
238	*Emmenanthe*	G-2	BBY(B)	HAL,PT,CO
240	*Encelia*	I-2/5	BUTT,TEPH,SYR, BBY(V),BEET(ML, CC),WASP	CMP!AN,HAL!AD! PR ++
242	*Epilobium*	G-1/3	SYR	HAL,PLY

244	Eremocarpus	?G	wind?+BUTT,WASP, BBY,TACH	HL!DI!PLY
245	Eriastrum	G-1/3	BBY(B,O)	PR,DN,HAL
246	Erigeron	I,G,A-?	BUTT!BBY(V)++	CMP!(OML),DN! PR!HAL!HY!
247	Eriodictyon	?-5	BUTT!BIRD!MASAR WASP	BB!ND!CL!AN!OS! HY
248	Eriogonum	G/I-1/5	WASP!BUTT,MUSC, BEET(MD,CR)BBY(O, V,B,A)	BB!PR!CT!HAL! HY!PRO!
249	Eriophyllum	G/I-3/5	BUTT!SYR,BEET (BP,CY),WASP	BB!HAL!AD!OS!
251	Eryngium	G-1/2	SYR,WASP,BBY,BUTT	HY!HAL!
252	Erysimum	?I-2/4	BIRD,SYR,BUTT	HAL!AD,PLY
254	Eschscholzia	G/I-1/2	BEET(ML,ME)	BB!DF,HAL!PR!
255	Eucnide	?	---	HS!PR!DI,PR!
257	Euonymus	I-1	---	DI,BB?
259	Euphorbia	?-1/3	WASP +	ND!PR!DI
270	Fouquieria	?-5	BIRD!	---
271	Fragaria	G-3	SYR,BBY(B),BEET (BP)	AD!NM,OS
272	Frankenia	G-1	---	DI,PLY
273	Frasera	?	WASP	BB!PLY
275	Fremontia	?	---	XY!PLY
276	Fritillaria	?	BIRD?	AD
281	Gaura	?	MOTH	---
282	Gayophytum	G-1/3	BBY!(B,V),SYR	AD,DF!PLY
283	Gentiana	G/I-3/5	---	BB!
284	Geraea	?	?	CMP!HAL!PR,HS
285	Geranium	G-1/3	SYR,BEET,WASP	BB!HAL!HY
286	Geum	G-1	MUSC	AD
287	Gilia	G-4	BBY!(B,O),BUTT!	DF!HAL!HP!OS! PLY
290	Glandularia	"I"-5	BUTT!	---
293	Glycyrrhiza	G-3	---	BB!OS!AN
295	Gnaphalium	?	BEET(MR),WASP!	HY!CT,DI
299	Grindelia	?-5	BUTT,BBY(V),BEET (ML)	CMP!BB!HAL!PLY
300	Gutierrezia	?-5	BBY(V),BUTT,WASP	CMP!CT!PR!HAL! PLY ++
302	Habenaria	G-1	MOSQ	---
303	Hackelia	G-3/5	SYR!BUTT,BBY(B)	OS,PLY
305	Haplopappus	I-5	BUTT!WASP!BBY(V)	CMP!BB!HAL!PR, PLY ++
309	Helenium	?	BUTT	CMP!BB!HAL!
310	Helianthella	I-5	BEET(BP,CY),BUTT TEPH	OS!SY,PLY

311	Helianthemum	G-1	---	HAL
312	Helianthus	I-5	BUTT!WASP! +	CMP!BB!HAL!PLY++
313	Heliotropium	G-1/3	BBY	AN!AS,HAL,ND,PR
315	Hemizonia	?-5	BBY(V),SYR,BUTT, BEET(ML)	AD,ML!XG!HAL!TP
316	Heracleum	?	SYR!MUSC	HAL,BB!
318	Hesperocallis	I-5	SPHINX	---
319	Hesperochiron	?G-3	---	OS,HP,CH,PLY,BB
326	Heteromeles	I-2	BEET(MD,D),WASP, SYR,BUTT	HY,HAL,PR,AD
327	Heterotheca	?-4	BEET(MD),BUTT	CMP!HAL!PR
328	Heuchera	?	PFLY!BBY(O),SYR	---
332	Hoffmannseggia	I-5	---	CN,BB,AN
337	Holodiscus	I-2	PFLY, BEET(MD,D)	HAL,HY,AD
339	Horkelia	G-1/3	BUTT!BBY,BEET(D)	PLY(HAL,HY,OS,AD) ND!
344	Hydrophyllum	?G-3	---	BB!
351	Hyptis	?I-5	BUTT,SYR,BBY(V), BIRD	PLY(OS,PR,HAL,AD)
354	Ipomopsis	G?-5	BIRD!	---
355	Iris	"I"-3/5	BIRD!BBY(A)	BB!OS!
356	Isomeris	I-5	BIRD	BB!HAL,SY,AN
365	Kalmia	I-4	---	BB!AD!OS!
366	Kelloggia	?G-2	BBY(O)!	PLY
369	Krameria	?	---	CN!
374	Larrea	"G"-5	+++	XY!CT!PR!HT!PLY +
375	Lasthenia	G/I-1/5	BBY(V)!BUTT!	AD!HAL!NM,AD +
376	Lathyrus	I-5	BUTT	BB!SY!OS!PLY
378	Layia	G/I-1/5	BUTT!BBY(V),SYR	AD!AD!HAL!
379	Ledum	I-1	BEET(MD),SAWF	BB!OS
383	Lepechinia	?-5	BIRD!BBY(A)	BB!OS!CR,AS
384	Lepidium	G-1/2	MUSC	PR!AD!HAL!
385	Lepidospartum	I-5	BUTT,WASP!	HAL!XY!PR,CMP! Θ(ML,MG)
386	Leptodactylon	I?-1	MOTH	---
387	Lesquerella	G-2	SYR!	AD
388	Lessingia	?I-5	BUTT!BBY!(V),SYR	CMP!(ΘMG),HAL
393	Ligusticum	G-3	MUSC,PWSP, BEET (MD)	HAL
396	Lilium	I-?	BIRD!SPHINX!	BB!
397	Limnanthes	G-4	BUTT	AD!PN!OS,PLY
400	Linanthus	G-3/5	BBY!(B,A),BUTT,SYR	AD,DF,PLY
401	Linum	G-1/4	BUTT	BB,PLY
406	Lithocarpus	"I"-5	wind +	CT!
407	Lithophragma	I,A-2	BBY(B)	AD,BB
409	Lobelia	?	BIRD	---

411	Lomatium	"G"-5	TACH,SYR,BEET,(MD),BUTT	AD!AD!HAL!
412	Lonicera	?	BIRD!	BB!EV,XY!
413	Lotus	I/G-1/5	BUTT	BB!OS!SY!ANT!
417	Lupinus	I/G-1/5	BUTT	BB!OS!SY!ANT!AN!EM!XY
418	Lycium	?	BIRD	AN,AN,HAL,ID
426	Machaeranthera	I-?	BUTT +	CMP!HAL!PR
428	Madia	G-2/5	BEET(BP),MOTH	HAL!CR,BB!
430	Malacothamnus	?-5	BEET(MD)	DD!HAL!PLY
431	Malacothrix	?-3/5	BBY!(O,V)	ND!AD!PR!HAL!PLY!DF!
435	Malvastrum	G-1	---	DD!
437	Marah	I-1	?GNATS	AD,BB
440	Meconella	?	---	AD,HAL!
442	Mentha	?	BUTT	BB!HAL!
443	Mentzelia	G-1/5	MOTH?	PR!BB!HAL!PLY,XR,PRT
446	Mertensia	G?-5	---	CT!BB,OS
447	Mesembryanthemum	?-5	WASP	BB!HAL!PLY
450	Microseris	G-2	BEET(BP!),SYR	AD,BB,HAL
451	Microsteris	G-1	BBY(B!)	---
452	Mimulus	G/I-1/5	BIRD!BBY(A)	OS!HP!DF!BB!MG
453	Mirabilis	?G-2	BIRD!SPHINX	HAL,PLY,AN
455	Mohavea	G-2	---	XR,PR
457	Monardella	?-5	BBY!(B,O,A),BUTT! BIRD!	BB!OS!DN,AS,AN,HY,ND
463	Montia	G-2	BBY(B),SYR	AD,NM
471	Nama	G-2/4	---	CO,ND,AS,AT
473	Navarretia	G-2	BBY(B)	PR,EX,PLY(ΘHAL)
476	Nemophila	G/I-1/5	SAWF!SYR	AD!AD!DF,PN!OS!AT,CL,NM
478	Nicotiana	G-3	SPHINX,BIRD	---
484	Oenanthe	G-3	MUSC,BEET(MD),SYR	HAL
485	Oenothera	I-5	SPHINX!	AD,HAL
486	Olneya	I-5	---	CN!CH!AS!
487	Opuntia	A,?-1/5	?	DD!AS,LT!HAL!
492	Orthocarpus	G/I-1/5	SYR,MOTH	BB!AD!HAL
494	Osmaronia	I-1	MUSC	AD
496	Oxalis	I,A-?	PFLY,BBY(B)	BB
504	Paeonia	G-2	---	AD,HAL

505 *Palafoxia*	?G-2	BUTT +	CMP!HAL!
509 *Parkinsonia*	I-5	---	BB,XY,CN
513 *Pectis*	G-3	BBY! +	CMP!PR!HAL,NO
515 *Pedicularis*	?-5	BIRD!BUTT	AN!BB
517 *Penstemon*	"I"-5	BIRD!MASAR!BBY (A)	OS!OS!AT!HP!BB! PLY +
521 *Perideridia*	G-4	WASP!BEET(MD), SYR,MUSC	HYL!PLY
523 *Petalonyx*	G-?	BBY(V,B,O),WASP	AS,PR,HAL
529 *Peucephyllum*	G?-2	---	PLY(ΘCMP)
530 *Phacelia*	G-5	MASAR!BUTT!BBY! SAWF!	ANT!AT!CH!CT!CO! AD!DF!HP!HS,BB! CL!HAL!OS!SY!XY
531 *Phalacroseris*	?	?	OS!PLY
532 *Philadelphus*	?-3	BEET(CY)	AD
533 *Phlox*	I-1	BUTT!MOTH!	---
536 *Pholistoma*	G-5	TENTH	AD!PLY
537 *Phoradendron*	I-1	PFLY	AD
539 *Phyllodoce*	?-5	SYR	BB!AD,OS,HAL,PLY
541 *Physalis*	?	---	PR,HM,CT,PLY
548 *Plagiobothrys*	G-2	BBY!(B,O),SYR	AD,HAL
551 *Platystemon*	I-3	SYR	AD!AD,HAL
552 *Plectritis*	?	BBY(B),SYR	OS,NM,HAL,PLY
554 *Pluchea*	?	?	MG,ML,AN,HAL,AS
558 *Polemonium*	G-2	---	BB!
569 *Potentilla*	G-1/5	MUSC!BBY!MOTH!	AD!ND!HAL,NM,HY, DF
571 *Proboscidea*	?	---	BB,PR,CN,AN
572 *Prosopis*	I-5	WASP!	CN!AS!CH!HAL!HY, PR +
574 *Prunus*	I-4	SYR,BEET(CY,D)	AD!HAL,HY,BB!NM
575 *Psathyrotes*	?	BBY!(V),TACH!	Θ(CMP)
580 *Psoralea*	?	?	CN!OS,BB!SY,AN
586 *Purshia*	?	---	BB!EM!AD!
590 *Rafinesquia*	?G-?	BBY(O)	AN,HS,NO
591 *Raillardella*	I-1/5	BEET(ME)	BB!OS!
592 *Ranunculus*	G-1/5	SAWF!PFLY!MUSC! BUTT!BEET(CY,BP) SYR	AD!AD!PN!HAL!
593 *Rhamnus*	I-5	WASP!SYR,BEET (CY)	AD!BB!HAL!HY! PR,PN
594 *Rhododendron*	I-5	BIRD,SPHINX! BBY(A)	BB!
595 *Rhus*	I-2/4	BEET(CY)	AD,BB,NM,HY,PR
596 *Ribes*	I-5	BIRD!	BB!AN!EM!OS!AD!

601	Rosa	G-4	BEET(BP,CY,D)	BB!CR,PLY
603	Rubus	A/G-2/5	BEET(CY,D)	BB!AD!HAL!OS!
609	Salazaria	?	BIRD	AN!HAL!
611	Salix	I-5	SAWF!WASP,SYR, BUTT	AD!AD!BB!HAL!NM, HY,PR
612	Salvia	?-5	BBY(B,A)!BIRD!	AN!AN!EM!OS!HAL! SY!
613	Sambucus	G-2	BEET(CY,MD!), WASP,PFLY,SAWF!	AD,CR
615	Sanicula	G/I-1/3	SYR!TACH!MOTH	AD!AD!HAL
620	Satureja	?	BIRD	BB!OS!PLY
621	Saxifraga	I/G/A-1/2	SYR	PLY
624	Scoliopus	I-1	MUSC	---
626	Scrophularia	I-5	BIRD!WASP!	BB!HAL!CR!HY,AD
627	Scutellaria	?	BIRD!	BB!OS!
628	Sedum	G-1/3	MUSC!	BB!OS!HAL!
629	Senecio	G/I-1/5	BUTT!SYR,BEET (BP),MUSC	CMP!BB!OS!PLY ++
636	Sidalcea	?-5	BEET(CY)	DD!SY,BB,HAL
637	Silene	G/I-1/2	MOTH,BIRD	---
639	Sisyrinchium	I/G-2/3	SYR!	HAL!
642	Smilacina	I-2	SYR!BBY(B)	AD!NM!
644	Solanum	G/?-1/4	BBY(B)	AN!BB!HAL!XY
645	Solidago	I-5	BUTT!WASP!TACH BBY(V,O),BEET(ME)	CMP!BB!HAL!HY,XY!+
649	Spergularia	G-1	SYR	HAL
650	Sphaeralcea	?-5	---	DD!CT!HAL!PLY
651	Sphenosciadium	G-5	WASP!MUSC!BEET (MD)	HY,HAL!BB!PLY
652	Spiraea	?-4	SYR	AD,BB
655	Stachys	?-5	BIRD?	BB!AN!XY,PLY
656	Stanleya	I-5	BUTT!	ND!BB!HAL!PLY
661	Stephanomeria	?-3	BUTT!BBY!(V)	CMP!AN!BB,HAL! TR,CR
662	Stillingia	?	WIND + WASPS	---
664	Streptanthus	?	BUTT,SYR	BB,AN,OS
672	Swertia	?	WASP!BEET(MD,D)	HY!HAL!PLY
674	Symphoricarpos	?-2	WASP,SPHINX	BB,HAL,PLY,DF
678	Taraxacum	A/?-2	SYR!	HAL!AD,OS
683	Teucrium	?	BIRD?	HAL
686	Thelypodium	?	---	ND,PR
687	Thermopsis	?	---	BB!OS,SY,XY

689	*Thysanocarpus*	G-2	SYR	AD
691	*Tidestromia*	G?-2	WASP,BBY	AS,EX,PR,ND
693	*Tofieldia*	?-3	BEET(CY!)	AD!
704	*Trichostema*	?-5	BIRD!WASP,BBY (B,O)	AN!AS!HAL!HY,MG, ML,SY,XY
705	*Trientalis*	I-2	SYR	HAL
706	*Trifolium*	G/I-1/5	BBY(B),BUTT	BB!ND!ANT!MG,OS! SY!DF
714	*Umbellularia*	I-1	BBY(B),TACH	BB!
717	*Vaccinium*	I-3	---	BB!OS
718	*Valeriana*	?-3	SAWF!SYR	PLY
721	*Veratrum*	?-1	WASP,MUSC,PWSP	BB
722	*Verbena*	"I"-5	BUTT!BBY(V)	PLY(BB,CR,MG,ML, OS)Θ(HAL)
726	*Vicia*	I-5	BUTT!	OS!SY!BB!ΘHAL
727	*Viguieria*	I-5	BUTT!WASP!BBY (V)	CMP!HAL,Θ(ML)
728	*Viola*	G/I-1/3	BBY!(B)	PLY(BB,OS,DI,AS)
730	*Whipplea*	?-2	BBY(B)	HAL
732	*Wislizenia*	?G-3	BUTT,WASP	PLY(HAL!BB,MG,ML, XY)
735	*Wyethia*	I-5	BUTT,SYR,BBY (B,A),BEET(CY!BP!)	OS!BB!MG!AD,HAL
739	*Yucca*	I-3	MOTH	---
741	*Zauschneria*	"I"-5	BIRD	---
742	*Zigadenus*	G-3	SYR	AD!

N.B. Results in this table represent general trends and are based on observations of a mere 2500 species plus the results of the bee catalogue. They are not meant to be taken as descriptive of yet unstudied species, though they may serve as bases for predictions.